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FOSSIL RECORD OF THE FICID GASTROPODS *UROSYCA*, *PRISCOFICUS*, AND *FICUS* FROM COASTAL-WESTERN NORTH AMERICA: PHYLOGENETIC AND GLOBAL PALEOBIOGEOGRAPHIC IMPLICATIONS[1]

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ABSTRACT. This is the first detailed paleontologic study of three ficid-gastropod genera that lived during the early to middle Cenozoic in shallow marine waters from Washington southward to northern Baja California, Mexico. The genera are: *Urosyca* Gabb, 1869, *Priscoficus* Conrad, 1866, and *Ficus* Röding, 1798. The latter is the senior synonym of *Ficopsis* Conrad, 1866. Nine species are recognized: middle Paleocene *Urosyca robusta* Weaver, 1905; middle to late Paleocene *Urosyca caudata* Gabb, 1869; early to middle Eocene *Priscoficus cooperiana* (Stewart, 1927) new combination, of which *Ficopsis meganosensis packardi* Merriam and Turner, 1937 is a junior synonym; middle to late Eocene *Priscoficus hornii* (Gabb, 1864) new combination; late middle to late? Eocene *Priscoficus cowlitzensis* (Weaver, 1912) new combination; early to middle Eocene *Ficus remondii* (Gabb, 1864) new combination, of which *Ficopsis remondii crescentensis* Weaver and Palmer, 1922 is a junior synonym; middle to late Eocene *Ficus mamillata* Gabb, 1864; late Eocene to early Oligocene *Ficus gesteri* Wagner and Schilling, 1923; and early Oligocene to early Miocene *Ficus modesta* (Conrad, 1848). *Ficopsis meganosensis* Clark and Woodford, 1927, and *Ficopsis furlongi* Palmer, 1923, are *nomen dubia*.

Urosyca is only known from California; northern Baja California, Mexico; and Australia. Its range is middle to late Paleocene. *Priscoficus* was widespread and ranges from late early Paleocene to late Eocene, with an early Miocene relictual species in western Europe. Both genera had amphitropic distribution in warm seas. The near extinction of *Priscoficus* coincided with global cooling near the end of the Eocene. The early Eocene forms of *Ficus* appear to be intermediate with *Priscoficus*. After most likely originating in England, *Ficus* became amphitropic and was widespread in warm seas bordering a broad equatorial gap. Through time, the spire height of *Ficus* decreased, its last whorl became more inflated, and its shell size increased. *Ficus* was diminished by the global cooling event near the end of the Eocene, but starting in Oligocene/Miocene time, it rebounded, greatly diversified, and began to spread into equatorial waters. During the Pliocene and Pleistocene, it occurred mainly in the New World.

INTRODUCTION

Ficid gastropods ("fig shells") are represented today nearly entirely by genus *Ficus* Röding, 1798, whose a dozen or so species live in tropical and, to a lesser extent, in temperate seas (Neo, 2010). Most are trawled from continental-shelf environments in water depths less than 350 m, but a few can live intertidally and burrow as the tide recedes (Verhaeghe and Poppe, 2000; Neo, 2010). Their shells are subject to postmortem transport and, in extreme cases, can be found admixed with the remains of nonmarine organisms along coastal-sabkha shorelines that are located many kilometers from the ocean (Squires and Thor, 1984). Species of *Ficus* probably spend much of their time crawling around and, when stationary, are partly to almost completely buried in sand (Beu, 1998:797). Although *Ficus* has been reported (Wilson and Gillett, 1971) as feeding on sea urchins and other echinoderms, these reports are anecdotal (Neo, 2010). Based on stomach contents, at least one species preys on polychaete worms (Warén and Bouchet, 1990). Sexes are separate, and sexual dimorphism occurs in shell length, where females are commonly larger than males (Neo, 2010).

Ficus today occurs principally in three malacological provinces: Indo-West Pacific, Caribbean, and Panamic (Abbott and Dance, 1982; Verhaeghe and Poppe, 2000). Species that range widely throughout the tropical Indo-West Pacific presumably have planktotrophic larvae, but at least one species evidently has direct development (Beu, 1998:798). According to Warén and Bouchet (1990:83), a planktotrophic larva of *Ficus* has never been reported, but they stated that planktotrophic development might be indicated by a few modern species.

Starting with the work of Conrad (1848, 1866) and of Gabb (1864, 1869), ficids have been recognized as occurring in the Cenozoic rock record of coastal-western North America, from Washington southward to northern Baja California, Mexico (Fig. 1). Although widespread in this region, ficid species are relatively uncommon but can be locally abundant. Their nearly continuous record in this region affords a significant opportunity to study their evolutionary succession during a 46-million-year interval, from middle Paleocene to early Miocene. The main purposes of this present article are to restudy the morphology of most of the coastal-western North America Cenozoic ficids, establish how many valid genera and species are represented, and update their biostratigraphy. Ancillary purposes are to gain insights to help understand the evolution and global paleobiogeography of these genera. To achieve this latter goal, it was necessary to undertake the first, comprehensive global review of fossil ficids.

Trophosycon Cooper, 1894, the only other Cenozoic ficid known with certainty from coastal-western North America, was not included in the present study. This genus, which is of early Miocene to early Pliocene age and is endemic to this area, has been studied in detail by Addicott (1970, 1976).

MATERIALS AND METHODS

The examined specimens are from fine-grained, argillaceous sandstone and siltstone. Specimens are mostly incomplete, and nearly all lack the anterior tip of the shell, as well as the full extent of the siphonal canal. Weathered specimens are common, and incomplete ones commonly resemble other weathered and incomplete gastropods, especially cassids. A high-speed drill with diamond-coated drilling wheels was used for cleaning. Morphologic terms are from Cox (1969).

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[1] URL: www.nhm.org/scholarlypublications

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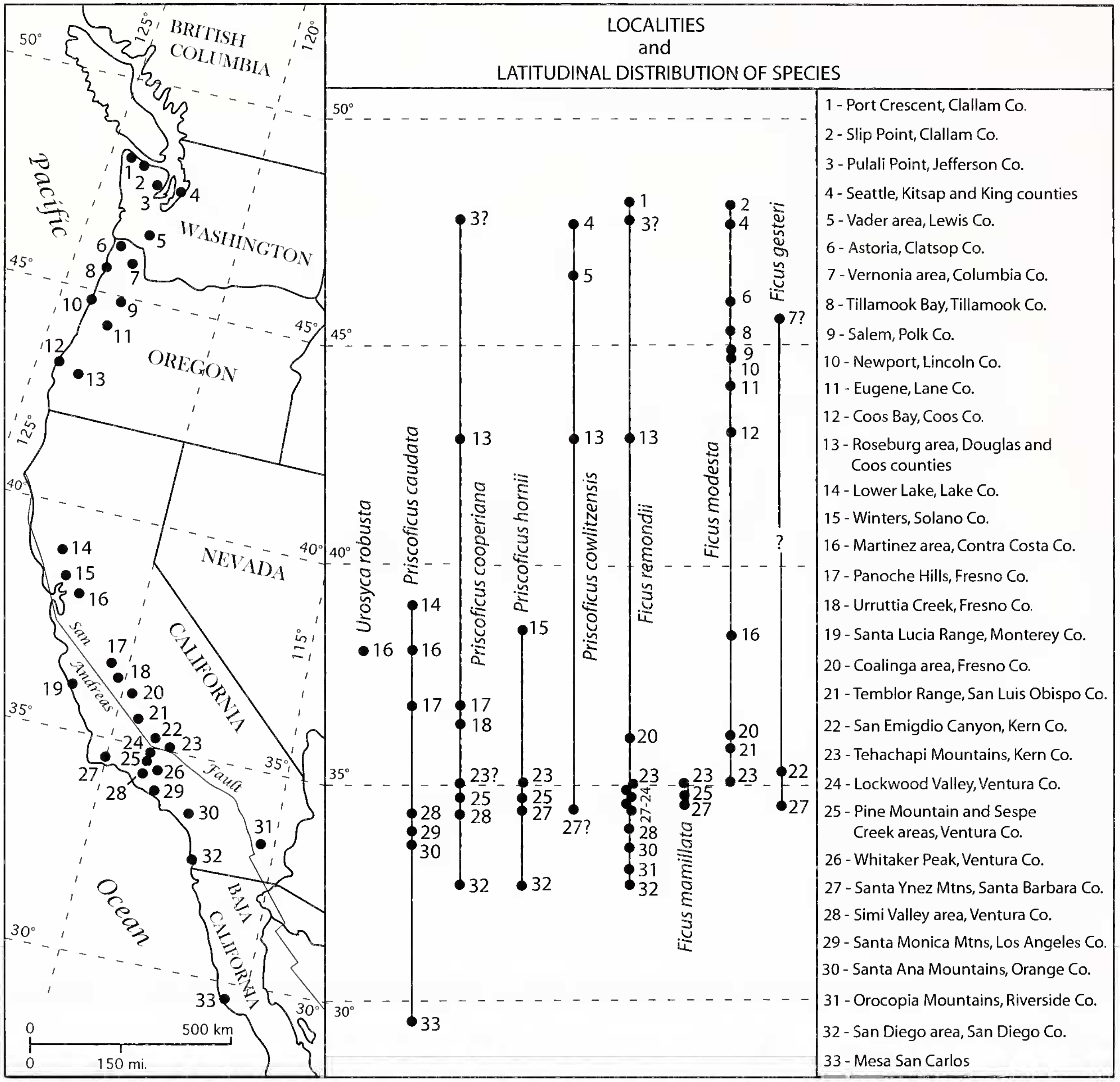

LOCALITIES
and
LATITUDINAL DISTRIBUTION OF SPECIES
BRITISH COLUMBIA
WASHINGTON
OREGON
NEVADA
CALIFORNIA
BAJA CALIFORNIA
Pacific Ocean
San Andreas Fault
50°
45°
40°
35°
30°
125°
120°
115°
0 500 km
0 150 mi.
Urosyca robusta
Priscoficus caudata
Priscoficus cooperiana
Priscoficus hornii
Priscoficus cowlitzensis
Ficus remondii
Ficus modesta
Ficus mamillata
Ficus gesteri
27-24
1 - Port Crescent, Clallam Co.
2 - Slip Point, Clallam Co.
3 - Pulali Point, Jefferson Co.
4 - Seattle, Kitsap and King counties
5 - Vader area, Lewis Co.
6 - Astoria, Clatsop Co.
7 - Vernonia area, Columbia Co.
8 - Tillamook Bay, Tillamook Co.
9 - Salem, Polk Co.
10 - Newport, Lincoln Co.
11 - Eugene, Lane Co.
12 - Coos Bay, Coos Co.
13 - Roseburg area, Douglas and Coos counties
14 - Lower Lake, Lake Co.
15 - Winters, Solano Co.
16 - Martinez area, Contra Costa Co.
17 - Panoche Hills, Fresno Co.
18 - Urruttia Creek, Fresno Co.
19 - Santa Lucia Range, Monterey Co.
20 - Coalinga area, Fresno Co.
21 - Temblor Range, San Luis Obispo Co.
22 - San Emigdio Canyon, Kern Co.
23 - Tehachapi Mountains, Kern Co.
24 - Lockwood Valley, Ventura Co.
25 - Pine Mountain and Sespe Creek areas, Ventura Co.
26 - Whitaker Peak, Ventura Co.
27 - Santa Ynez Mtns, Santa Barbara Co.
28 - Simi Valley area, Ventura Co.
29 - Santa Monica Mtns, Los Angeles Co.
30 - Santa Ana Mountains, Orange Co.
31 - Orocopia Mountains, Riverside Co.
32 - San Diego area, San Diego Co.
33 - Mesa San Carlos

Figure 1 Localities and latitudinal distribution of coastal-western North America *Urosyca*, *Priscoficus*, and *Ficus* species.

The Paleocene and Eocene provincial molluscan "stages" used in Figure 2 are informal (in quotation marks), stem from Clark and Vokes (1936), and apply to California and northern Baja California. The Oligocene and Miocene stages are formal (not in quotation marks) and apply mostly to Washington and Oregon. Squires (2003) discussed the history of the derivation of these stages and provided a list of which formation is correlative to which stage. For a few additional formations, especially the upper Oligocene and Miocene ones, the reader is referred to Prothero (2001).

Much of the material used in this study is housed in the Natural History Museum of Los Angeles County (LACMIP). Information about its localities can be accessed through the LACMIP website link: http://ip.nhm.org/ipdatabase/locality_show. Information about the Museum of Paleontology, Berkeley (UCMP), type localities can be accessed through the website link: http://ucmpdb.berkeley.edu.

In compiling the synonymies presented here, citations accompanied by illustrations are the rule. A few that did not have accompanying illustrations were cited because useful taxonomic, morphologic, and/or geologic comments were provided. Reports of ficids based solely on a megafaunal list were not used in the synonymies but were cited in the "Stratigraphic Distribution" sections. New stratigraphic occurrences of ficids detected during the course of this present investigation are indicated as "new information" in the "Stratigraphic Distribution" sections.

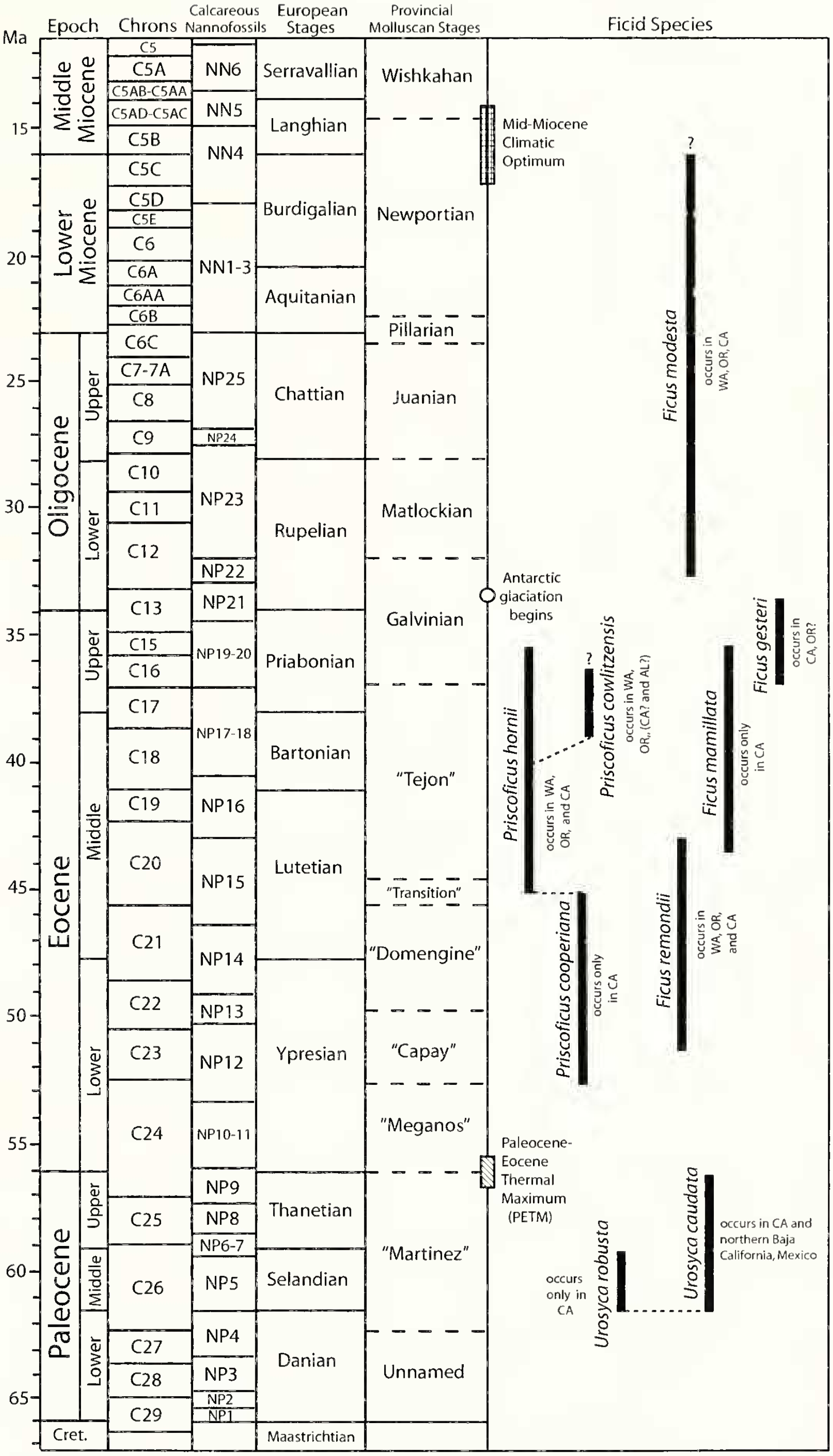


Figure 2 Chronostratigraphic ranges of coastal-western North America species of *Urosyca*, *Priscoficus*, and *Ficus*. Geologic time scale, European stage boundaries, and paleomagnetic chrons/polarities from Gradstein et al. (2012:figs. 2.2, 28.9); coastal-western North America provincial molluscan stages based on (Squires, 2003:fig. 2.1). Timing of climatic events from Gradstein et al. (2012:fig. 28.11). Dashed lines indicate evolutionary lineages.

Tables 1–3, which list species of ficids from throughout the world, were based on a comprehensive but not exhaustive literature search. It was mandatory that an illustration be found of every species detected in the literature. The present writer's placement of these species into the various available genera of ficids relied heavily on these illustrations.

Two *nomen dubia* were detected. One is the so-called "*Ficopsis meganosensis*" Clark and Woodford (1927:112–113, pl. 19, figs. 18–20), based on three incomplete and weathered steinkerns (internal molds) most likely from uppermost Paleocene to lowermost Eocene strata in California. The holotype is from a different locality than the paratypes, and the exact stratigraphic positions and geographic locations of these localities are unknown. Oleinik (1997:pl. 4, figs. 5–12) used the name "*F. meganosensis*" for possibly several species from the lower Paleocene Getkilninskaya Formation at Cape Getkilnin, Kamchatka. Oleinik (2001:text-fig. 4) and Oleinik and Marincovich (2003:table 3) also listed "*Ficopsis meganosensis*" from the upper middle Eocene lower member of the Snatolskaya Formation (equivalent to the "Tejon Stage") in northwest Kamchatka.

The other *nomen dubium* is the so-called "*Ficopsis furlongi*" Palmer (1923:295, pl. 52, fig. 6), based on a single specimen from the lower Eocene Capay Formation, near Vacaville, Solano County, California. The specimen is missing its spire and is crushed. Stewart (1927:379) reported accurately that this "badly crushed specimen will not permit a conclusive study." More specimens are needed to ascertain whether or not this taxon is even a ficid.

ABBREVIATIONS

Locality and/or catalog numbers

ANSP	Academy of Natural Sciences at Drexel University, Philadelphia
CAS	California Academy of Sciences San Francisco
LACM	Natural History Museum of Los Angeles County, Malacology Section
LACMIP	Natural History Museum of Los Angeles County, Invertebrate Paleontology Department
UCMP	University of California Museum of Paleontology, Berkeley
UO	University of Oregon Museum, Eugene
UWBM	University of Washington Burke Museum

SYSTEMATICS

Class Gastropoda Cuvier, 1797

Subclass Caenogastropoda Cox, 1959

Superfamily Ficoidea Meek, 1864

REMARKS. Ficids were commonly assigned (e.g., Wenz, 1941; Boss, 1982; Warén and Bouchet, 1990) to superfamily Tonnoidea Suter, 1913, before Riedel (1994) placed ficids in Ficoidea. A few workers (e.g., Solsona, 1999; Verhaeghe and Poppe, 2000), however, continued to place ficids in Tonnoidea. Zou et al. (2011) reported that based on molecular phylogenetics, tonnoideans and Ficidae form a monophyletic clade as the sister group to the neogastropods. Bouchet and Rocroi (2005:250) recognized only Ficidae within superfamily family Ficoidea.

Family Ficidae Meek, 1864

[= Pyrulidae Swainson, 1840:307 = Sycotypidae Gray, 1853:38 = Ficulidae Carpenter, 1857:453–454 = Thalassocyonidae Riedel, 1994:457].

REMARKS. Meek (1864:19) provided no comments or discussion concerning his proposal of the name "Ficidae." According to Bouchet and Rocroi (2005:77), Meek used the name in place of Pyrulidae Swainson, 1840, based on *Pyrula* Lamarck, 1799. It seems likely that Meek proposed his replacement name because *Pyrula* Lamarck, 1799 was erroneously used by some early workers (e.g., Reeve, 1847; Sowerby, 1880) for gastropods belonging to non-ficid families that have members with similar pyriform and/or ficoid shapes. The name Ficidae has won general acceptance, and, as noted by Bouchet and Rocroi (2005), Meek's name is conserved under ICZN (1999:46) Article 40.2. *Ficus* Linnaeus, 1753, is also a genus of angiosperm "fig-tree" plants.

Genera regarded here as belonging to family Ficidae are the following, listed in chronological order of naming: *Ficus* Röding, 1798; *Priscoficus* Conrad, 1866; *Urosyca* Gabb, 1869; *Trophosycon* Cooper, 1894; *Thalassocyon* Barnard, 1960; and *Bulbificopsis* Squires and Saul, 2003. The geologic ranges of these genera are shown in Figure 3.

Ficid shells are mostly less than 70 mm in height, but some are up to 160 mm in height. Their shells are pyriform, fusiform, or rarely pagodiform in shape. Whorls are few. The spire, which can be angulate or non-angulate, is very low to moderately high, and the spire angle is narrow to wide. The last whorl is large and can bear one to four carinae, or none. Ornament commonly consists of a fine to coarse (rarely stronger) reticulate combination of spiral and axial ribs/riblets. Nodes (blunt or spinose) can occur at intersections of the spiral and axial components. Ornament can consist only of spiral ribs/riblets. The columella is smooth. The long and generally straight siphonal canal commonly twists (turns) slightly to the left and bears a weak (rarely stronger) siphonal fasciole. The growth line is orthocline to opisthocline, with a parasigmoidal flexure (adapertural bend) commonly present near the suture. On *Priscoficus* and *Ficus*, the protoconch is low conical, pauspiral, with 1.5–2 whorls that are smooth and show gradual transition to the spirally striate earliest teleoconch whorl.

There are relatively few morphologic characters to distinguish species of ficids. These characters, which can be variable and gradational, are: last-whorl shape, spire height, number and spacing of carinae, spacing and strength of nodes or tubercles on the carinae, and spacing and strength of primary spiral ribs, as well as for spiral riblets (striae) in the interspaces. Additionally, wide variation in these characters can occur among individuals of a species and even between dorsal and ventral sides of the same specimen. Overnaming of species is a common problem.

Ficids have been reported by many workers (e.g., Davies, 1935; Wenz, 1941) as ranging from Late Cretaceous to Holocene, and the Late Cretaceous report is based on *Pirula* (*Protopirula*) *capensis* Rennie (1930:222, pl. 25, figs. 21–23) from South Africa. Kiel and Bandel (2003:458, figs. 4.7, 4.8) synonymized *Protopirula* Rennie, 1930, with the cypraeid *Cypraea* Linnaeus, 1758, and reported that Rennie's species is based on juvenile specimens of approximately middle Santonian to early Campanian age. The earliest confirmed record of ficids is the Late Cretaceous ("mid" Maastrichtian) *Bulbificopsis garza* Squires and Saul (2003:54–55, figs. 2.8–2.11) from California.

The extant Thalassocyonidae Riedel, 1994, consists of a single genus, the extant *Thalassocyon* Barnard, 1960. Warén and Bouchet (1990) showed that only a single species, *Thalassocyon bonus* Barnard, 1960, is known and that it occurs in abyssal depths from South Africa eastward to northern New Zealand. Beu (1969) reported that *Thalassocyon* is a ficid based on shell morphology, radula, and reduced periostracum. Its pagodiform shell shape and upturned peripheral spines on the shoulder of the last whorl, however, are quite different from any living or extinct ficid. Additionally, Thalassocyonidae has a calcareous operculum (Beu, 1969), whereas other ficids, however, do not have an operculum (Boss, 1982:1011).

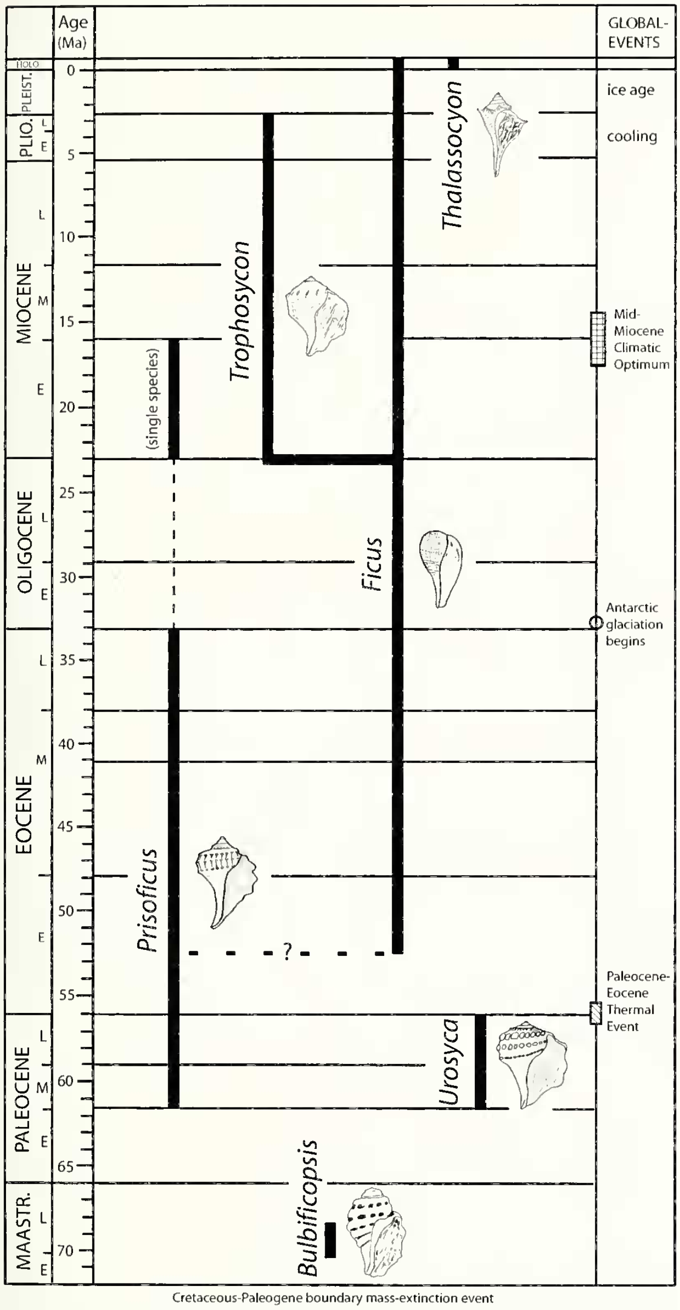


Figure 3 Genera that comprise family Ficidae and their geologic ranges. Sketches based on type species of each genus. Range information sources: Squires and Saul (2003) for *Bulbificopsis*; herein for *Urosyca*, *Priscoficus*, and *Ficus*; Addicott (1970) for *Trophosycon*; and Bernard (1960) for *Thalassocyon*. Geologic time scale and timing of climatic events from Gradstein et al. (2012).

Genus *Urosyca* Gabb, 1869

TYPE SPECIES. *Urosyca caudata* Gabb, 1869, by monotypy; middle to late Paleocene, California and northern Baja California, Mexico.

DIAGNOSIS. Shell size up to height 70 mm (incomplete), pyriform, last whorl quadrate (blocky shape) with sutural welt, spire very low (approximately 14 percent of shell height), spire angle 115°, four carinae with nodes on last whorl, spiral riblets/striae cover shell.

REMARKS. Stewart (1927:380–381), without giving any reasons, reassigned the type species of *Urosyca* to genus *Priscoficus* Conrad, 1866, thereby making *Urosyca* a junior synonym of the poorly defined genus *Priscoficus*. The present writer, however, recognizes *Urosyca* as a valid genus because it differs from *Priscoficus* in the following ways: larger shell, much lower spire, much wider last whorl with a blocky rather than a narrow cylindrical shape, presence of a sutural welt on the last whorl, and absence of thin, prominent axial ribs connecting the nodes on the spiral carinae on the last whorl.

Urosyca robusta Weaver, 1905
Figures 4–7

Urosyca robusta Weaver, 1905:119, pl. 13, fig. 1; Dickerson, 1914:151, pl. 15, fig. 8.

EMENDED DESCRIPTION. Shell size up to height 52.7 mm and diameter 28 mm (same dorsoventrally crushed incomplete specimen with siphonal canal missing). Shell pyriform, neck constricted, last whorl wide, quadrate. Protoconch missing. Teleoconch of nearly three whorls. Spire very low, can be nearly depressed. Last whorl with sutural welt and four noded carinae; carinae uniformly spaced; nodes smaller in size and increasing in number on most anterior carina. Spiral riblets cover shell; mature specimens also with prominent spiral riblet in middle of interspaces between carinae. Columella smooth. Siphonal canal long and straight. Growth line unknown.

TYPE. Holotype UCMP 11886, UCMP loc. 243 (Vine Hill Sandstone near Martinez, California).

GEOLOGIC RANGE. Middle Paleocene (Selandian); equivalent to provincial "Martinez Stage" (lower part).

STRATIGRAPHIC DISTRIBUTION. Vine Hill Sandstone (lower part) near Martinez, Contra Costa County, California (Weaver, 1953, as *Priscofusus* [sic] *robusta*).

REMARKS. The examined material of this rare species consisted of two specimens. Although both are internal molds (steinkerns), they show unique morphology. The four rows of spiral ribs bearing nodes/tubercles serve to distinguish it from *Urosyca caudata*, which has three rows. *Urosyca robusta* also differs from *U. caudata* in the following ways: shell larger, spire lower, sutural welt narrower, presence of prominent spiral riblet in middle of interspaces between carinae, and large specimens have fewer and less swollen nodes. It is not possible to count the full number of nodes on the carinae of the examined specimens of *U. robusta* because of adhering rock matrix and/or weathered areas. Figures 5–7 are the first photographs of the holotype.

Urosyca caudata Gabb, 1869
Figures 8–15

Urosyca caudata Gabb, 1869:159, 221, pl. 27, fig. 38; Stanton, 1896:1047, pl. 67, fig. 6; Cossmann, 1904:124–125, fig. 14 [facsimile reproduction of Gabb's figure]; Dickerson, 1914:151, pl. 15, figs. 7a, b.

Priscoficus caudatus (Gabb). Stewart, 1927:379–380, pl. 25, fig. 7; Schenck and Keen, 1940:pl. 20, fig. 6 [reproduction from Dickerson, 1914:pl. 15, fig. 7a]; Shimer and Shrock, 1944:500, pl. 205, fig. 12 [reproduction from Stewart, 1927:pl. 25, fig. 7]; Weaver, 1953:29; Zinsmeister, 1983a, pl. 3, figs. 20, 21; 1983b:1293, 1294, fig. 3C–E; Zinsmeister and Paredes-Mejia, 1988, pl. 1, figs. 3, 4, 7?, 8.

EMENDED DESCRIPTION. Shell size up to height 70 mm and diameter 59 mm (same dorsal-ventrally crushed incomplete specimen, siphonal canal missing). Shell wide pyriform, neck constricted. Posterior half of last whorl quadrate in shape. Protoconch missing. Teleoconch of 3.5 whorls. Suture undulatory, somewhat concealed. Spire low (approximately 14 percent of shell height). Spire angle approximately 115°. Last half of last whorl can be deviantly coiled at low angle, producing short angulation occupied by sutural welt on adult specimens larger than diameter 15.5 mm; sutural welt can have node-like swollen irregularities. Ornament consisting of three spiral carinae bearing strong nodes and spiral striae; interspaces between carinae can have microscopic reticulate ornamentation consisting of growth lines intersecting with spiral striae. Small patches of nodes can be present along suture of penultimate whorl. Last whorl with three carinae; somewhat uniformly spaced, with most anterior two slightly more closely spaced; interspaces concave between carinae. First carina (on shoulder) bearing approximately 21 nodes/tubercles on mature specimens (10 on immature specimens); approximately 27 nodes/tubercles on second carina; approximately 30 nodes/tubercles on third carina. Nodes become progressively smaller on succeeding carinae. Nodes/tubercles on third carina becoming increasingly less distinct near outer lip. First and second carinae bear broadly swollen areas extending axially short distance anteriorly but not reaching subsequent carina. Spiral striae, moderately widely spaced and non-reticulate, cover last whorl and neck. Columella smooth. Aperture wide posteriorly. Siphonal canal long, bends to left, and slightly twisted anteriorly. Growth line orthocline.

TYPE. Lectotype ANSP 4208, designated by Stewart (1927), most likely from Vine Hill Sandstone near Martinez, Contra Costa County, California.

GEOLOGIC RANGE. Middle Paleocene (Selandian) to upper Paleocene (Thanetian); equivalent to provincial "Martinez Stage" (lower and upper parts).

GEOGRAPHIC RANGE. California to northern Baja California, Mexico.

STRATIGRAPHIC DISTRIBUTION. MIDDLE PALEOCENE ("MARTINEZ STAGE"): Martinez Formation, Lower Lake, Lake County, California (Stanton, 1896; Weaver, 1953); Vine Hill Sandstone (lower part) near Martinez, Contra Costa County, California (Weaver, 1953); Santa Susana Formation (lower part), Meier Canyon, Simi Hills, south side Simi Valley, Ventura County, California (Zinsmeister, 1983a, 1983b); Silverado Formation, Santa Ana Mountains, Orange County, California (LACMIP loc. 10452, new information); Sepultura Formation, Mesa San Carlos, northern Baja California, Mexico (Zinsmeister and Paredes-Mejia, 1988). UPPER PALEOCENE ("MARTINEZ STAGE"): Vine Hill Sandstone (upper part) near Martinez, Contra Costa County, California (Weaver, 1953); Lodo Formation (basal part), near junction of Silver and Panoche creeks, Fresno County, California (Smith, 1975); Santa Susana Formation, Palisades Highlands, Santa Monica Mountains, Los Angeles County, California (Squires and Kennedy, 1998); Santa Susana Formation, east side Stone Canyon Reservoir, Santa Monica Mountains, Los Angeles County, California (LACMIP loc. 23304, new information).

REMARKS. The examined material consisted of 57 specimens. Preservation is poor, and all specimens are incomplete, especially pertaining to the anterior end of the siphonal canal. Although a slight twist is present on the siphonal canal of the specimen illustrated in Figures 11–13, only a hint of a siphonal fasciole is preserved. All the specimens are internal molds (steinkerns), except the specimen shown in Figures 11–13, and all have three carinae. Most specimens show some signs of being dorsal-ventrally crushed, especially the largest ones. Nearly three-fourths of the specimens are from the Santa Susana Formation, Simi Valley, California. The largest ones (e.g., Figs. 14, 15) are from the Palisades Highlands in the Santa Monica Mountains, California. A careful analysis of Weaver's (1953:29, pl. 3D) faunal list and accompanying geologic map with localities plotted revealed that both *U. caudata* and *U. robusta* occur close together geographically and stratigraphically in the lower part of the Paleocene Vine Hill Sandstone. *Urosyca caudata* also occurs in the upper part of the Vine Hill Sandstone, but *U. robusta* does not.

The angle of view of the Southern California specimen of *Priscoficus caudata* shown by Zinsmeister (1983a:pl. 3, fig. 30; 1983b:fig. 3C) gives the false appearance that the siphonal canal is curved, but this curvature pertains only to the shell area just anterior to the widest part of the last whorl, not to the siphonal canal, which is actually straight on more complete specimens (Figs. 8, 9). The northern Baja California specimen identified as *P. caudata* by Zinsmeister and Paredes-Mejia (1988:pl. 1, fig. 7) is very unusual in having only two carinae on the last whorl and having nearly obsolete nodes on the carinae. It is likely that this specimen is badly weathered.

The low spire of *P. caudata* is similar to that of *Priscoficus smithii* (Sowerby, 1827:151, pl. 578, figs. 1, 2, not 3) from the lower Eocene London Clay in England. Wrigley (1929:236–238, pl. 15, figs. 1a, b; 2a, b) also provided illustrations and comments regarding this species. *Priscoficus caudata* differs by having a sutural welt and more swollen nodes. The low spire of *P. caudata* is also similar to that of *Priscoficus triserialis* Whitfield (1865:260, unfigured) from lower Eocene strata in Alabama. Gardner (1939:29–30, pl. 7, fig. 19) figured this species. *Priscoficus caudata* differs by having a sutural welt.

The present writer places *Levifusus*? *quadrifunifer* Darragh (1997:76–77, figs. 3S–U), from Paleocene strata in Victoria, southeast Australia, in genus *Urosyca*. Darragh's species is remarkably similar to *U. caudata*, but *U. caudata* differs by having stronger nodes and a less bent siphonal canal. Darragh (1997) reported that his species has four prominent carinae on the last whorl, but his illustrations clearly show only three. The posterior-most "carina" is a sutural welt.

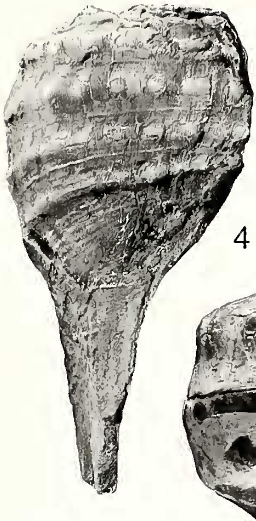
Urosyca caudata resembles the adult specimen figured by Marshall (1917:454–455, pl. 35, fig. 23) of *Proficus obtusa* (Marshall, 1917) from lower Paleocene to upper middle Eocene (Beu and Maxwell, 1990) strata in New Zealand. *Urosyca caudata* differs by having a lower, smaller, and non-inflated spire; narrower and less concave ramp; and a sutural welt. *Urosyca caudata* resembles the adult specimen of *P. obtusa* figured by Finlay and Marwick (1937:pl. 10, fig. 2) but differs by having a narrower ramp and a sutural welt. *Urosyca caudata* does not resemble the small specimen of *P. obtusa* figured by Marshall (1917:pl. 25, fig. 22) nor the adult specimen figured by Finlay and Marwick (1937:pl. 10, fig. 1). It seems that *P. obtusa*, which is the type species of genus *Proficus* Finlay and Marwick, 1937, is a composite of at least two different taxa. Pending rectification of this situation, the taxonomic status of *Proficus* is uncertain. Squires (2011:1208) reported that *P. obtusa* resembles *Pyropsis louellae* Squires (2011:figs. 3.1–3.3) of Late Cretaceous age from California.

Genus *Priscoficus* Conrad, 1866

[= *Fulguroficus* Sacco, 1890]

TYPE SPECIES. *Pirula intermedia* Melleville, 1843, by subsequent designation (Stewart, 1927); late Paleocene, France.

DIAGNOSIS. Shell size up to height 42 mm, fusiform, last whorl cylindrical, suture can be canalicuate on spire, spire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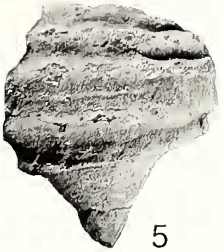
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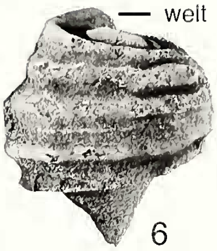

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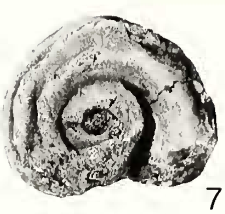
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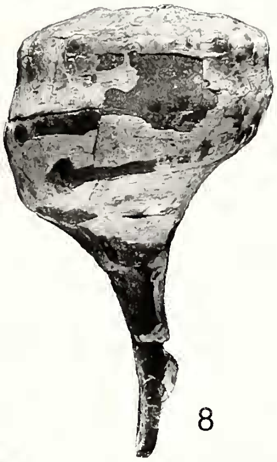
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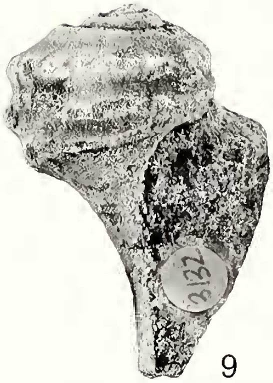
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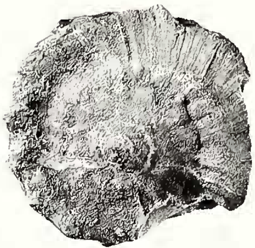
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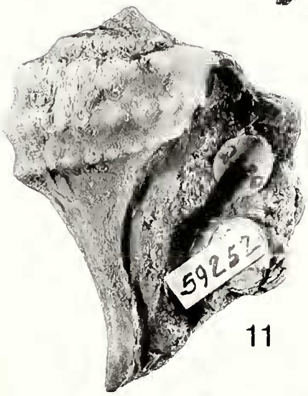
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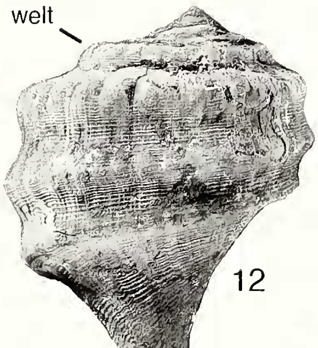

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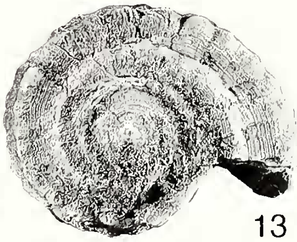
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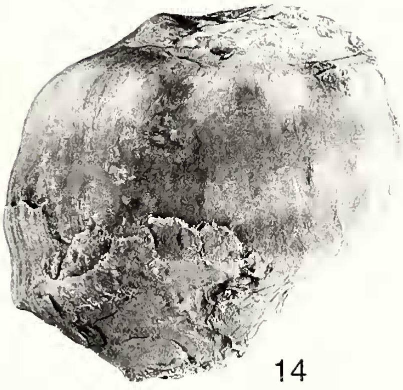
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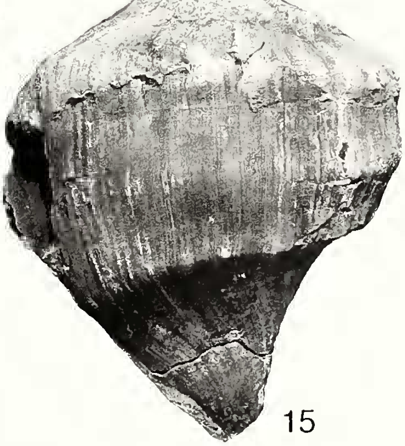
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Figures 4–15 *Urosyca* species from coastal-western North America. **4–7.** *Urosyca robusta* Weaver, 1905 (Vine Hill Sandstone). **4.** Hypotype UCMP 11865, UCMP loc. 1888, left-lateral view, height 53.5 mm, ×1.2; **5–7.** Holotype UCMP 11886, UCMP loc. 243, abapertural view, height 22.7 mm, ×1: **5.** abapertural view; **6.** abapertural view, slightly oblique; **7.** apical view. **8–15.** *Urosyca caudata* Gabb, 1869. **8.** Lectotype ANSP 4208, Martinez, California (Vine Hill Sandstone), abapertural view, height 54.5 mm, ×1.1; **9.** Hypotype LACMIP 14472, LACMIP loc. 23132 (Santa Susana Formation, Simi Hills), height 35 mm, ×1.6; **10.** Hypotype LACMIP 14473, LACMIP loc. 16869 (Santa Suana Formation, Santa Monica Mountains), apical view, maximum diameter 40 mm, ×0.8; **11–13.** Hypotype LACMIP 10978, LACMIP loc. 22330 (Santa Susana Formation, Simi Hills), height 37 mm, ×1.4: **11.** apertural view; **12.** abapertural view; **13.** apical view; **14–15.** Abapertural views of geronitic individuals, LACMIP loc. 10689 (Santa Susana Formation, Santa Monica Mountains): **14.** hypotype LACMIP 14474, height 52 mm, ×1; **15.** hypotype 14475, height 70 mm, ×0.9.

moderately low (approximately 25 percent of shell height), spire angle approximately 84°, ramp concave to sloped, three to four carinae with nodes (can be spinose) on last whorl, reticulate ornament prominent, growth line slightly opisthocline (rarely orthocline on ramp) and with or without parasigmoidal flexure near suture.

REMARKS. The name *Priscoficus* was proposed in a footnote by Conrad (1866:100) who mentioned that *Pirula intermedia* Melleville (1843:115, pl. 10, figs. 8, 9) of late Paleocene age (Thanetian) from France and *Murex smithii* Sowerby (1827:11, pl. 578, figs. 1, 2, not 3) of Eocene age from England might both belong to genus *Priscoficus*. Conrad (1866) did not give any diagnostic characters nor any description of *Priscoficus*. Stewart (1927), who designated *P. intermedia* as the type species of *Priscoficus*, also did not provide any diagnostic morphologic characters. Gardner (1939:30), and Harzhauser (2002:91, pl. 5, figs. 14, 15) used *Fulguroficus* as a subgenus of *Priscoficus*.

Del Río (2012:1006–1007, figs. 3.7, 3.8) reported *Priscoficus* cf. *P. gracilis* (Wilckens, 1905) from lower Paleocene (Danian Stage) rocks in Patagonia, Argentina. The positive generic assignment of *P.* cf. *P. gracilis*, however, cannot be determined because the material consists of incomplete, internal molds (steinkerns). Del Río (2012), furthermore, reported that the Patagonian *P.* cf. *P. gracilis* closely resembles *Pyropsis gracilis* Wilckens found by Furque and Camacho (1949:pl. 4, fig. 11) in Cretaceous and Paleocene strata in Argentina. The generic assignment of the specimen illustrated by the latter workers, however, also cannot be determined because the specimen is incomplete and appears to be a steinkern.

Collignon (1951:118, pl. 19, figs. 1, 1a) reported *Tudicla gracilis* (Wilckens, 1905) from Cretaceous strata in Madagascar, but the specimen is an incomplete steinkern.

Priscoficus cooperiana (Stewart, 1927) new combination

Figures 16–19

Fusus (*Hemifusus*) *cooperii* Gabb, 1864:86, pl. 28, fig. 207. Not *Fusus cooperi* Conrad, 1834:148.

Perissolax cooperii (Gabb). Conrad, 1865b:363.

Ficopsis cooperii Gabb. Dickerson, 1915:61–62, pl. 6, fig. 11; Dickerson, 1916:438, pl. 37, fig. 7 (same specimen as Dickerson, 1915:pl. 6, fig. 11); Clark, 1929:pl. 9, fig. 13.

Ficopsis cooperiana Stewart, 1927:378, 379 [new name for *Fusus* (*Hemifusus*) *cooperii* Gabb, 1864, preoccupied]; Moore, 1968:26, pl. 11, fig. b; Givens, 1974:81, pl. 9, figs. 7, 9; Squires, 1984:29–30, fig. 8a.

Ficopsis meganosensis packardi Merriam and Turner, 1937:102, pl. 6, fig. 7; Turner, 1938:83, pl. 15, figs. 22, 26, 27; Vokes, 1939:153, pl. 19, figs. 11, 13; Weaver, 1942:400–401, pl. 77, fig. 14.

EMENDED DESCRIPTION. Shell size up to height 37.2 mm and diameter 17.2 mm (on a nearly complete specimen). Shell fusiform. Protoconch missing. Teleoconch of approximately 3.5 whorls. Suture flush, can be canaliculated on spire whorls. Spire moderately low (approximately 22 percent of shell height). Spire angle approximately 80°. Ramp shallowly concave. Teleoconch covered by fine spiral striae that can form reticulate pattern where crossed by growth lines; pattern variable from whorl to whorl and specimen to specimen; neck area prone to having spiral striae stronger than growth lines. More prominent ornament consisting of carinae bearing nodes. Penultimate whorl with two carinae bearing approximately 13 small, spinose nodes; posterior carina projected; anterior carina commonly obscured or partly obscured by sutural area. Last whorl with three carinae, approximately uniformly spaced; interspaces concave between carinae. Carinae with eight to 10, widely spaced hollow nodes; on larger specimens, nodes become obsolete toward outer lip. Posterior carinae (on shoulder) with posteriorly pointing, spinose nodes, slightly stronger than on other two carinae. Aperture narrow, outer lip shows tricarinate outline. Columella smooth. Siphonal canal long and straight, slightly twisted anteriorly. Growth line slightly opisthocline on last whorl face, opisthocline (rarely orthocline) on ramp, with no parasigmoidal flexure near suture.

TYPES. Of *Fusus* (*Hemifusus*) *cooperii* Gabb, 1864, and of *Ficopsis cooperiana* Stewart, 1927, holotype UCMP 11691, UCMP loc. 2226 (Ardath Shale, San Diego, California). Of *Ficopsis meganosensis packardi* Merriam and Turner, 1937, holotype UCMP 33180, UCMP loc. A-662 (White Tail Ridge Formation, Roseburg area, Oregon).

GEOLOGIC RANGE. Middle lower Eocene (middle Ypresian) to lower middle Eocene (upper Ypresian); equivalent to provincial "Capay Stage" to "Transition Stage."

GEOGRAPHIC RANGE. Southwestern Oregon to Southern California; Washington?.

STRATIGRAPHIC DISTRIBUTION. MIDDLE LOWER EOCENE ("CAPAY STAGE"): Questionably in Crescent Formation, Pulali Point, Jefferson County, Washington (LACMIP loc. 41510, new information); White Tail Ridge Formation, Roseburg area, Douglas County, Oregon (Merriam and Turner, 1937); Lodo Formation, Cerros Shale Member, Urruttia Canyon, north of Coalinga, Fresno County, California (Vokes, 1939, as the Arroyo Hondo Formation); tentatively from Tejon Formation, Uvas Conglomerate Member, East Twin Creek, Tehachapi Mountains, Kern County, California (Addicott in Nilsen, 1987). UPPER LOWER TO LOWER MIDDLE EOCENE ("DOMENGINE STAGE"): Domengine? Formation, Panoche Hills, Fresno County, California (LACMIP loc. 10302, new information); Juncal Formation, south of Wegis Ranch, Pine Mountain area, Ventura County, California (Givens, 1974); Llajas Formation, Simi Valley, Ventura County, California (Squires, 1984); Ardath Shale and Scripps Formation (lower part), San Diego County, California (Givens and Kennedy, 1979). MIDDLE EOCENE ("TRANSITION STAGE"): Scripps Formation (upper part), San Diego County, California (Givens and Kennedy, 1979).

REMARKS. The examined material consisted of 56 specimens. Preservation is generally good, especially in the Ardath Shale. At several localities in the White Tail Ridge Formation, Juncal Formation, Llajas Formation, and Ardath Shale, *Priscoficus cooperiana* co-occurs with *Ficopsis remondii*.

Plafker (1974) listed *Ficopsis* cf. *F. meganosensis packardi* as being present in the Tokun Formation on Wingham Island, Gulf of Alaska. According to Tucker and Feldmann (1990:441), Plafker's checklist pertains to the upper Eocene basal part of the formation. Confirmation of this report is beyond the scope of the present report.

Devyatilova and Volobueva (1981:119, pl. 3, figs. 13, 14) illustrated two non-apertural views of a specimen of *Ficus* (*Ficopsis*) *meganosensis packardi* from the Getkilnin Formation on the shore of Penzhin Inlet, Kamchatka. Their specimen is a steinkern whose spire is missing. More and better preserved specimens are needed to ascertain the identification of this gastropod.

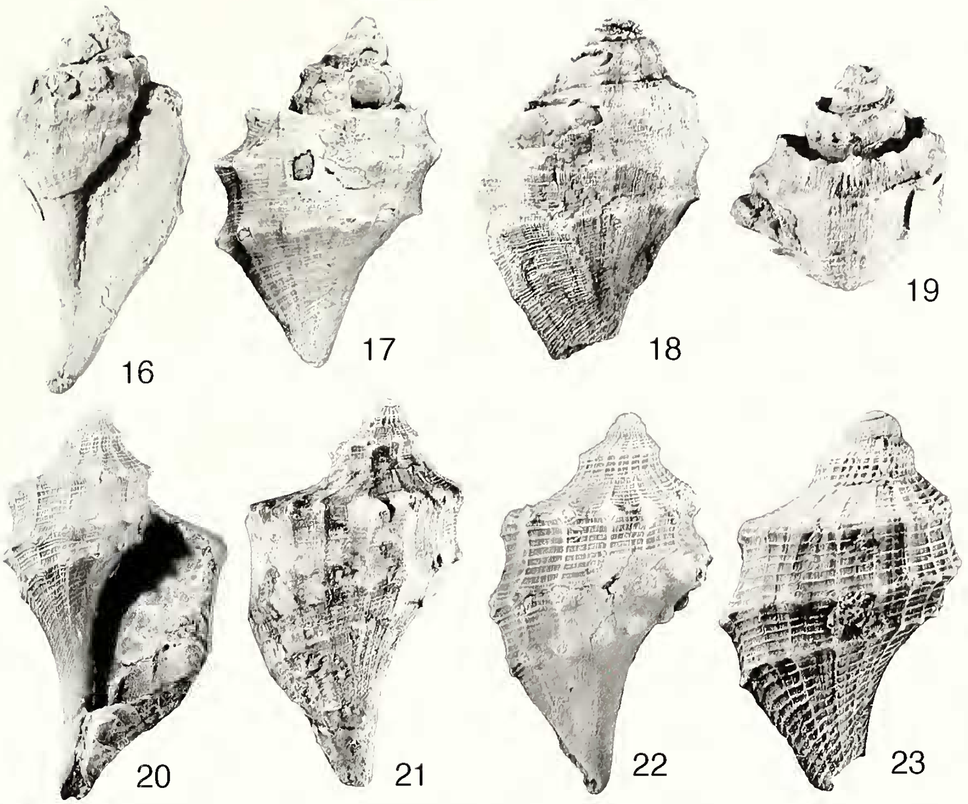
Priscoficus hornii (Gabb, 1864) new combination

Figures 20–23

Fusus (*Hemifusus*) *hornii* Gabb, 1864:86, pl. 28, figs. 206, 206a.

Perissolax hornii (Gabb). Conrad, 1865b:363.

Ficopsis hornii Gabb. Dickerson, 1915:61–62, pl. 6, fig. 9; Anderson and Hanna, 1925:111–112, pl. 12, fig. 8; Stewart, 1927:377–378, pl. 30, figs. 3, 4; Schenck and Keen, 1940:pl.



Figures 16–23 *Priscoficus* from coastal-western North America. **16–19.** *Priscoficus cooperiana* (Stewart, 1927), new combination. **16.** Holotype UCMP 33180 of *Ficopsis meganosensis packardi* Merriam and Turner, 1937, UCMP loc. A662 (White Tail Ridge Formation), apertural view, height 37.3 mm, ×1.4; 17. Hypotype UCMP 11691 of *Ficopsis cooperi* (Gabb, 1864), UCMP loc. 2226 (Ardath Shale), abapertural view, height 27.5 mm, ×1.7; **18.** Paratype UCMP 33636 of *Ficopsis meganosensis packardi* Merriam and Turner, 1937, UCMP loc. 3608 (White Tail Ridge Formation), abapertural view, height 28 mm, ×1.6; **19.** Hypotype LACMIP 14476, LACMIP loc. 22312 (Llajas Formation), slightly oblique abapertural view, height 12.3 mm, ×2.4. 20–23. *Priscoficus hornii* (Gabb, 1864), new combination. **20–21.** Hypotype LACMIP 14477, LACMIP loc. 22340 (Tejon Formation, Liveoak Shale Member?), height 35 mm, ×1.5: **20.** apertural view; **21.** abapertural view. **22.** Hypotype LACMIP 14478, LACMIP loc. 22340 (Tejon Formation, Liveoak Shale Member?), abapertural view, height 25.4 mm, ×2; 23. Hypotype LACMIP 14479, LACMIP loc. 7155 (Tejon Formation, Liveoak Shale Member), abapertural view, height 15 mm, ×3.3.

26, fig. 1 [reproduction from Dickerson, 1915:pl. 6, fig. 9]; Weaver and Kleinpell, 1963:191, pl. 26, fig. 1; Givens, 1974:81, pl. 9, fig. 10; Squires, 1994:48, pl. 2, figs. 3, 14.

Ficopsis hornii cowlitzensis (Weaver). Clark, 1929:pl. 14, figs. 8, 11.

Ficopsis cowlitzensis (Weaver). Clark, 1938:709, pl. 3, figs. 1, 7.

EMENDED DESCRIPTION. Shell size up to height 42 mm and diameter 25.5 mm (on an incomplete specimen with spire mostly missing). Shell fusiform. Protoconch low conical, paucispiral, approximately 1.25–1.5 whorls, smooth with gradual transition to spirally striate earliest teleoconch whorl. Teleoconch of approximately three whorls. Suture flush. Spiral moderately low (approximately 25 percent of shell height). Spire angle approximately 86°. Ramp shallowly concave. Teleoconch covered by fine reticulated ornament consisting of thin spiral riblets intersecting with growth lines and also with thin, widely spaced axial riblets. Axial riblets form nodes where intersecting with carinae. Spire whorls with medial angulation. Angulation weak but distinct on ante-penultimate whorl; angulation on penultimate whorl nodose with approximately 18 small nodes, each one connected to axial riblet on accompany ramp; second row of nodes on penultimate whorl can be partially visible along suture. Last whorl with three carinae, two most anterior ones more closely spaced; interspaces concave between carinae. Carinae bear spinose nodes, connected from carina to carina by prominent, slightly raised thin axial riblets; nodes can be knob-like, especially on ventral surface of shell; knobs commonly broken off, leaving hollow areas (pits). Carina on shoulder with approximately 12 prominent nodes; medial carina with 11 nodes, slightly weaker than on shoulder; anterior carina with 10 nodes, weaker than those on other carinae and showing tendency to become obsolete toward outer lip. Aperture moderately narrow. Outer lip unthickened and showing tricarinate outline. Columella smooth. Siphonal canal long, straight, narrowly notched, and very slightly twisted anteriorly. Growth line slightly opisthocline, with no parasigmoidal flexure near suture.

TYPE. Lectotype ANSP 4182, exact location unknown, Tejon Formation, near Fort Tejon, Kern County, California.

GEOLOGIC RANGE. Middle Eocene (middle Lutetian Stage) to middle upper Eocene (middle Priabonian Stage); equivalent to provincial "Transition Stage" to "Galvinian Stage."

GEOGRAPHIC RANGE. California.

STRATIGRAPHIC DISTRIBUTION. MIDDLE EOCENE ("TRANSITION STAGE"): Tejon Formation, Uvas Conglomerate Member, Liveoak Canyon, Tehachapi Mountains, Kern County, California (Addicott in Nilsen, 1987); Juncal Formation (upper part), Pine Mountain area, Ventura County, California (Givens, 1974). MIDDLE EOCENE ("TRANSITION STAGE" OR "TEJON STAGE"): Tejon Formation, Liveoak Shale Member, Liveoak Canyon, Tehachapi Mountains, Kern County, California (Addicott in Nilsen, 1987). MIDDLE EOCENE ("TEJON STAGE"): Markley Formation, just southwest of Winters, Solano County, California (Clark, 1938); Tejon Formation (undifferentiated), Edmonston Pumping Plant, Tehachapi Mountains, Kern County, California (Addicott in Nilsen, 1987); Matilija Sandstone, Pine Mountain area, Ventura County, California (Givens, 1974); Coldwater Sandstone and Circle B Sandstone Member of Cozy Dell Shale, Sespe Creek area, Ventura County, California (Squires, 1994); Mission Valley Formation, San Diego County, California (Givens and Kennedy, 1979). UPPER EOCENE (GAVINIAN STAGE): undifferentiated Sacate-Gaviota formations, Nojoqui Creek, Santa Ynez Mountains, Santa Barbara County, California (Weaver and Kleinpell, 1963).

REMARKS. The examined material consisted of 153 specimens. Preservation is generally very good. *Ficopsis hornii* closely resembles *Ficopsis cooperiana*, but the former differs by having a taller first teleoconch whorl that is also angulate and not rounded, fewer and more widely spaced nodes, and more closely spaced spiral threads. *Ficopsis hornii* also shows no indication of having canaliculated spire whorls.

Priscoficus cowlitzensis (Weaver, 1912) new combination

Figures 24–28

Hemifusus cowlitzensis Weaver, 1912:45, pl. 1, figs. 1, 4.
Ficopsis cowlitzensis (Weaver). Dickerson, 1915:61, pl. 6, fig. 10; Davies, 1935:fig. 390; Turner, 1938:93, pl. 15, fig. 21; Clark, 1938:709, pl. 15, fig. 21; pl. 3, figs. 1, 7; Weaver, 1942:399–400, pl. 77, figs. 3, 5, 6, 8, 9, 11.

EMENDED DESCRIPTION. Shell size up to height 42.2 mm and diameter 27.5 mm (on an incomplete specimen with siphonal canal missing). Shell fusiform. Protoconch low conical, paucispiral, approximately 1.5 whorls, smooth with gradual transition to spirally striate earliest teleoconch whorl. Teleoconch of approximately three whorls. Suture flush. Spire moderately low (approximately 22 percent of shell height). Spire angle approximately 85°. Ramp shallowly concave. Teleoconch covered by fine reticulate ornament consisting of thin spiral riblets intersecting with growth lines and also with thin, widely spaced axial riblets. Axial riblets form nodes where intersecting with carinae. Spire whorls with angulation on anterior third of whorl; angulation weak but distinct on ante-penultimate whorl and bearing approximately 22 closely spaced knob-like to spinose nodes, each connecting to axial riblet on accompanying ramp. Last whorl with three carinae, two most anterior ones more closely spaced. Carinae with nodes, connected from carina to carina by prominent slightly raised thin axial riblets; nodes knob-like on ventral surface, spinose on dorsal surface; carina on shoulder with approximately 23 small nodes; medial carina with approximately 20 very slightly weaker nodes; anterior carina with approximately 20 nodes weaker than on other carinae. Aperture moderately wide, outer lip unthickened and showing tricarinate outline. Columella smooth with thin callus on medial part. Siphonal canal long, very slightly flexed, bends slightly upward dorsally, narrowly notched, and twisted anteriorly. Siphonal fasciole weak. Growth line slightly opisthocline, with parasigmoidal flexure present near suture.

TYPES. Holotype UW 27 (CAS 7615), UW loc. 232 (Cowlitz Formation, Washington); paratype UW 27-A (CAS 7615-A), UW loc. 232 (Cowlitz Formation, Washington).

GEOLOGIC RANGE. Upper middle Eocene (middle Bartonian) to questionably lower upper Eocene (middle Priabonian); equivalent to provisional "Tejon Stage" (upper part) to questionably Galvinian Stage.

GEOGRAPHIC RANGE. Washington to southwest Oregon; Southern California?.

STRATIGRAPHIC DISTRIBUTION. UPPER MIDDLE EOCENE ("TEJON STAGE"): Tukwila Formation, King County, Washington (Nesbitt, 1998); Cowlitz Formation, Vader area, Lewis County, Washington (Weaver, 1912, 1942; Davies, 1935; Nesbitt, 1995); Coaledo Formation, west of Roseburg area, Coos County, Oregon (Weaver, 1942). QUESTIONABLY UPPER EOCENE (GALVINIAN STAGE): Gaviota Formation, Jalama Ranch, western Santa Ynez Mountains, Santa Barbara County (LACMIP loc. 7201, new information).

REMARKS. The examined material consisted of 363 specimens. Preservation is generally excellent, and most of the specimens are from the so-called "Big Bend" locality along the banks of the Cowlitz River, just east of Vader, Washington. Many specimens from this locality can be easily and entirely cleaned from their matrix. Protoconchs are commonly preserved. A questionable specimen, a steinkern, was detected from the Gaviota Formation in Santa Barbara County, California. If this occurrence is *Ficopsis cowlitzensis*, it would be the youngest and southernmost occurrence of this species.

Priscoficus cf. *P. cowlitzensis* [as *Ficopsis*] was tentatively reported (Wolfe, 1977:5) from the upper middle Eocene (upper part of the "Tejon Stage") in the upper Eocene basal Tokun Formation in the southern Alaska. More work on this possible occurrence needs to be done, but confirmation is beyond the scope of the present report.

Genus *Ficus* Röding, 1798

[= *Pyrula* Lamarck, 1799; *Pirula* Montfort, 1810 (unjustified emendation of *Pyrula*); *Ficula* Swainson, 1835; *Sycotypus* Gray, 1847; *Ficopsis* Conrad, 1866; *Fusoficula* Sacco, 1890; *Gonysycon* Woodring, 1959; *Diconoficus* Covacevich and Frassinetii, 1983].

TYPE SPECIES. *Murex ficus* Linnaeus, 1758:752 [= *Bulla ficus* (Linnaeus) of Linnaeus, 1767:1184 = *Bulla ficus* (Linnaeus) of Gmelin, 1791:3426 = *Murex ficus* Linnaeus of Gmelin, 1791:3545 = *Ficus communis* Röding, 1798 (name subsequently used by many authors for species not equivalent to *Murex ficus*, see "Remarks" below)], by tautonymy and subsequent designation of Dall (1906:296); Holocene, Indo-West Pacific.

DIAGNOSIS. Shell size up to height 160 mm, fusiform to pyriform, spire very low (barely perceptible) to moderately low (approximately 25 percent of shell height), spire angle 68°–140°, whorls rounded (except for geologically earliest forms having no carinae or up to three carinae without nodes), reticulate ornament prominent, interspaces variable in width and in number of spiral riblets, growth line opisthocline (commonly very slightly), with parasigmoidal flexure present near suture.

REMARKS. Klein (1753) first used the name "*Ficus*," but his usage was pre-Linnaean. For additional comments regarding the complex history of the naming of *Ficus*, see Dall (1909:74), Hollister (1958:69–70), and Beu (2010:313). The name "*Ficus*" is unusual in that it is a feminine noun with *-us* termination.

There has been much confusion about the usage of the name "*Ficus communis*." Röding (1798:148) equated his *Ficus* *communis* with *Bulla ficus* as used by Gmelin (1791). When Dall (1906:296), subsequently designated the type species of *Ficus*, he clearly indicated that he was referring to Gmelin's *B. ficus*, a name now referred to as *Ficus ficus* for a species confined to the Indo-Pacific region. The name "*Ficus communis*" should no longer be used, yet subsequent workers (e.g., Abbott, 1974:170) have commonly used the name "*Ficus communis*" for a ficid species living in waters from North Carolina to the Gulf of Mexico. Verhaege and Poppe (2000:15, 22), however, believed that Abbott (1974) should have used the name *Ficus papyratia* (Say, 1822). According to Verhaege and Poppe (2000), *F. papyratia* is a "complex of species" found only along the east coast of the United States and in the Caribbean Sea region. They also believed that *Ficus variegata* Röding, 1798, a species commonly put into synonymy with *F. ficus* and also found in the Indo-Pacific region, is a distinct species from *F. ficus*.

Conrad (1866) proposed the name *Ficopsis* in a very brief statement and, just as for *Priscoficus*, did not give any diagnostic characters nor any description of *Priscoficus*. He did list *Hemifusus hornii*, *H. cooperii*, *H. remondii*, and *Ficus mamillatus* as members of this genus. *Hemifusus hornii* and *H. cooperii* are now known to belong to *Priscoficus*, characterized by its quadrate last whorl with prominent wide-spaced ornamentation that is noded on nearly all species. No worker has doubted that *F. mamillatus* belongs to *Ficus*. The genus name *Ficopsis* Conrad (1866:100), which has been commonly applied to *H. hornii* and *H. cooperii* (see synonymies given herein), as well as to other Eocene ficids found throughout the world, however, has been a source of taxonomic confusion. As discussed below, the considerable range in morphologic characters of *Ficus* encompass those of *Ficopsis*, which is recognized here as a junior synonym of *Ficus*.

The protoconch of *Ficus* has been illustrated and discussed by several workers (e.g., Smith, 1907:pl. 17; 1945:236–237, pl. 1, figs. 1–8; Verhaeghe and Poppe, 2000:pls, 20–23; Beu, 2010:312, pl. 78, figs. 7–9).

The morphology of *Ficus* involves four variable shell features: spire height, inflatedness of last whorl, ornament, and size. As discussed later in this report, the evolution of the shell of *Ficus* reflects subtle changes involving these four variables.

Ficus remondii (Gabb, 1864) new combination

Figures 29–38

Fusus (*Hemifusus*) *remondii* Gabb, 1864:87, 211, pl. 18, fig. 36.

Ficopsis angulatus Weaver, 1905:119, pl. 13, fig. 5.

Fusus remondii Gabb. Arnold, 1907:pl. 39, figs. 7, 7a (figures reprinted in Eldridge and Arnold, 1907:figs. 7, 7a).

Ficopsis remondii angulata Weaver. Dickerson, 1914:85; Stewart, 1927:377.

Ficopsis remondii (Gabb). Dickerson, 1915:61–62, pl. 6, fig. 8; Stewart, 1927:376, pl. 30, figs. 1, 2; Turner, 1938:92–93, pl. 15, fig. 20; Schenck and Keen, 1940:pl. 26, fig. 3 [reproduction from Dickerson, 1915:pl. 8, fig. 8]; Deméré et al., 1979:pl. 2, fig. 4.

Ficopsis (*Ficopsis*) *remondi* (Gabb). Wenz, 1941:1081, figs. 3076a, b [reproductions from Stewart, 1927:pl. 30, figs. 1, 2]; Weaver, 1942:398–399, pl. 77, figs. 12; Kleinpell and Weaver, 1963:191, pl. 26, fig. 2.

Ficopsis remondi (Gabb). Shimer and Shrock, 1944:500, pl. 205, figs. 15, 16 [reproductions from Gabb, 1864:pl. 18, fig. 36].

Ficopsis remondii var. *crescentensis* Weaver and Palmer, 1922:39–40, pl. 11, fig. 14 [new name for *Ficopsis angulatus* Weaver, 1905, preoccupied]; Weaver, 1942:399, pl. 77, fig. 10.

Ficopsis remondii crescentensis Weaver and Palmer. Turner, 1938:93, pl. 15, fig. 19; Vokes, 1939:152–153; Givens, 1974:82, pl. 9, fig. 11; Squires, 1984:30, fig. 8b; Squires 1987:41, fig. 53; Squires, 1988:14, fig. 33; Squires, 2008:fig. 25.

Ficopsis crescentensis Weaver and Palmer. Stewart, 1946:pl. 11, fig. 17.

Ficopsis remondi crescentensis Weaver and Palmer. Moore, 1968:26, pl. 11, fig. c.

Ficopsis remondii crescentensis? Weaver and Palmer. Squires, 1991:pl. 2, fig. 3.

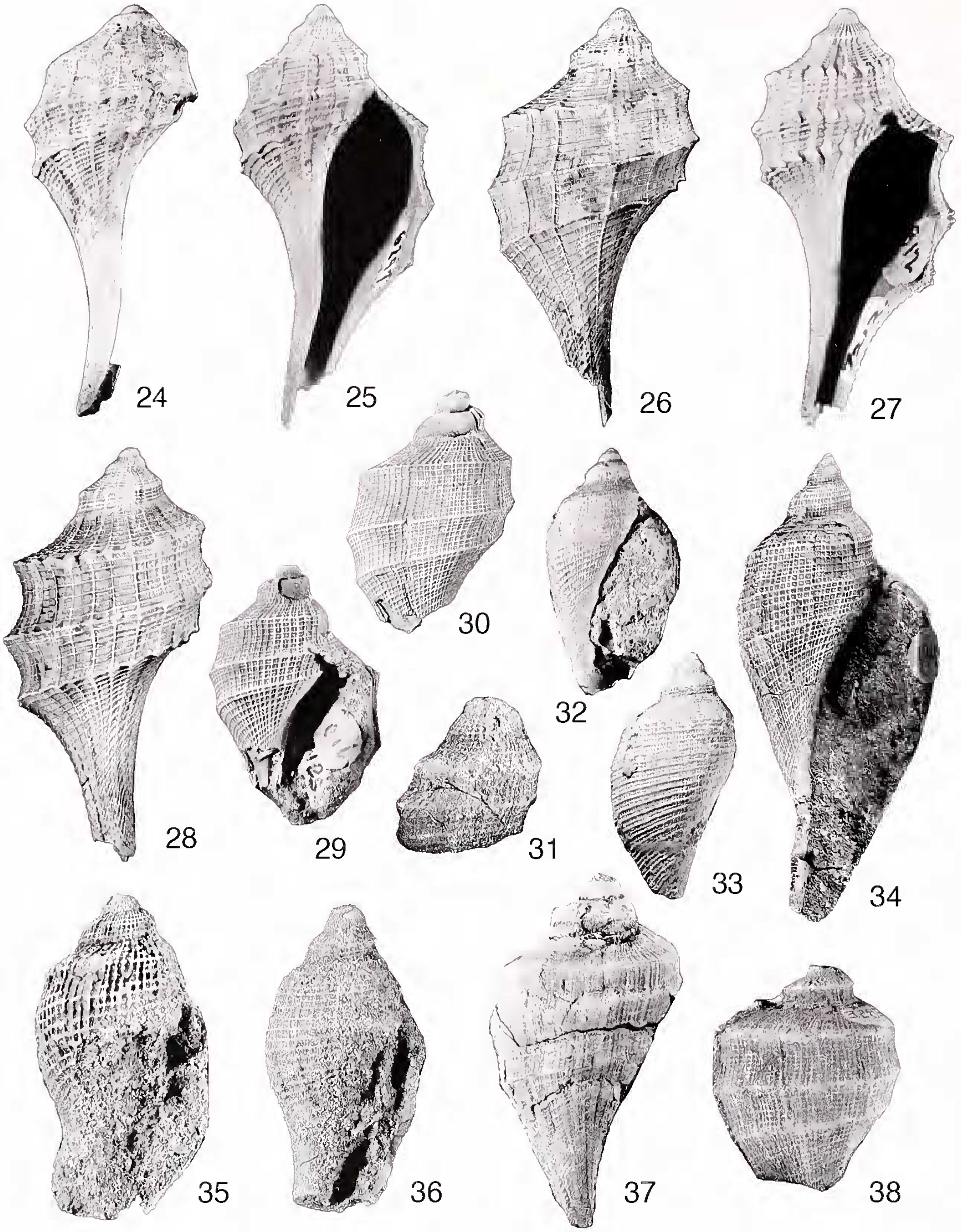
EMENDED DESCRIPTION. Shell size up to height 60.3 mm and diameter 24.7 mm (on a nearly complete specimen). Shell fusiform. Protoconch low conical, paucispiral, approximately 1.5–2 whorls, smooth with gradual transition to spirally striate earliest teleoconch whorl. Teleoconch of approximately three whorls. Suture weakly impressed to flush. Spire moderately low (approximately 25 percent of shell height). Spire angle approximately 68°. Ramp sloped. Teleoconch covered by uniformly fine reticulate ornament consisting of intersecting moderately thin spiral and axial riblets. Spire whorls with angulation either on medial or anterior third of whorl; angulation becoming stronger (carinate) with growth and most prominent on shoulder of last whorl. Last whorl spiral-rib ornament highly variable: no carinae, unicarinate, bicarinate, or tricarinate with two most anterior carinae more closely spaced. All carinae without nodes. Aperture moderately narrow, outer lip unthickened and showing tricarinate outline. Columella smooth. Siphonal canal long, straight, narrowly notched, and slightly twisted anteriorly. Siphonal fasciole weak. Growth line opisthocline, with parasigmoidal flexure present near suture.

TYPES. Of *Fusus* (*Hemifusus*) *remondii* Gabb, 1864, lectotype ANSP 4184, designated by Stewart (1927:376), Tejon Formation, north of Fort Tejon, Kern County, California. Of *Ficopsis angulatus* Weaver, 1905, holotype UCMP 11887 ("3 mi. south of Martinez," California *fide* Keen and Bentson, 1944:157). Of *Ficopsis remondii* var. *crescentensis* Weaver and Palmer, 1922, holotype UW 205 [= CAS 7616], UWBM loc. 358 (Crescent Formation, Port Crescent, Washington).

GEOLOGIC RANGE. Middle lower (middle Ypresian Stage) to lower middle Eocene (middle Lutetian Stage); equivalent to provincial "Capay Stage" to "Tejon Stage."

GEOGRAPHIC RANGE. Washington to Southern California.

STRATIGRAPHIC DISTRIBUTION. MIDDLE LOWER EOCENE ("CAPAY STAGE"): Crescent Formation, Port Crescent, Clallam County, Washington (Weaver and Palmer, 1922); White Tail Ridge Formation, Roseburg area, Oregon; Juncal Formation (lower part), Whitaker Peak, Ventura and Los Angeles counties, California (Squires, 1987); Maniobra Formation, Orocopia Mountains, Riverside County, California (Squires, 1991). UPPER LOWER EOCENE (near "CAPAY STAGE"/"DOMENGINE STAGE" boundary): Possible steinkern from Crescent Formation, Pulali Point, Jefferson County, Washington (LACMIP loc. 41511, new information); UPPER LOWER EOCENE TO MIDDLE EOCENE ("DOMENGINE STAGE"): Avenal Sandstone, south of Coalinga, Kings County, California (Kappeler et al., 1984); Avenal Sandstone, Reef Ridge, Coalinga area, Kings County, California (Stewart, 1946); Juncal Formation (upper part), Lockwood Valley, Ventura County, California (Squires, 2000); Matilija Formation, Pine Mountain area, Ventura County, California (Givens, 1974); Juncal Formation (upper part), Whitaker Peak, Ventura and Los Angeles counties, California (Squires, 1977, 1987); Matilija Sandstone?, Whitaker Peak, Ventura and Los Angeles counties, California (Squires, 1987); Llajas Formation, Ventura and Los Angeles counties, California (Squires, 1984); Santiago Formation, Santiago Canyon, Santa Ana Mountains, Orange County, California (Schoellhamer et al., 1981); Ardath Shale and Scripps Formation (lower part), San Diego County, California (Givens and Kennedy, 1979). MIDDLE EOCENE ("TRANSITION STAGE"): Friars Formation (upper



Figures 24–38 *Priscoficus* and Eocene *Ficus* species from coastal-western North America. **24–28.** *Priscoficus cowlitzensis* (Weaver, 1912), new combination (Cowlitz Formation). **24.** Hypotype LACMIP 14480, LACMIP loc. 22563, left-lateral view, height 31.9 mm, ×1.8; **25–26.** Hypotype LACMIP 14481, LACMIP loc. 6297, height 32.6 mm, ×2.5: **25.** apertural view; **26.** abapertural view. **27–28.** Hypotype LACMIP 14482, LACMIP loc. 7212, height 33.5 mm, ×1.8: **27.** apertural view; **28.** abapertural view. **29–38.** *Ficus remondii* (Gabb, 1864), new combination. **29–30.** Hypotype LACMIP 14483, LACMIP loc. 7185 (Ardath Shale), height 27.3 mm, ×1.2: **29.** apertural view; **30.** abapertural view. **31.** Holotype UCMP 11887 of *Ficopsis angulatus* Weaver, 1905, UCMP loc. 337 (unnamed formation near Martinez), abapertural view, height 4.8 mm, ×4.5. **32–33.** Plasto-hypotype UCMP 31388, UCMP loc. 148 (Tejon Formation), height 28.4 mm, ×1.2: **32.** apertural view; **33.** abapertural view. **34.** Hypotype LACMIP 14484, LACMIP loc. 40374 (Llajas Formation), apertural view, height 54 mm, ×1.2; **35.** Hypotype LACMIP 14485, LACMIP loc. 40373 (Llajas Formation), apertural view, height 16.7 mm, ×2.8; **36.** Hypotype LACMIP 14486, LACMIP loc. 40374 (Llajas Formation), apertural view, height 12.9 mm, ×3.6; **37.** Hypotype LACMIP 14487, LACMIP loc. 17150 (Llajas Formation), abapertural view, height 37 mm, ×1.4; **38.** Hypotype LACMIP 14488, LACMIP loc. 3285 (Tejon Formation, Liveoak Shale Member), abapertural view, height 34.8 mm, ×0.9.

part), San Diego, San Diego County, California (Squires and Deméré, 1991); Scripps Formation (upper part), San Diego County, California (Givens and Kennedy, 1979). MIDDLE EOCENE ("TRANSITION STAGE" OR "TEJON STAGE"): Tejon Formation, Liveoak Shale Member, Liveoak Canyon and Tejon Formation (undifferentiated), Edmonston Pumping Plant, Tehachapi Mountains, Kern County, California (Addicott in Nilsen, 1987); Matilija Sandstone, Nojoqui Creek Area, Santa Ynez Mountains, Santa Barbara area, Santa Barbara County, California (Weaver and Kleinpell, 1963). LOWER MIDDLE EOCENE ("TEJON STAGE"): Tejon Formation, Metralla Sandstone Member, Liveoak Canyon, Tehachapi Mountains, Kern County, California (Dickerson, 1915; Addicott in Nilsen, 1987); Mission Valley Formation, San Diego, San Diego County, California (Deméré et al., 1979; Givens and Kennedy, 1979).

REMARKS. The examined material consisted of 122 specimens. Preservation is generally moderately good to good. There is considerable variation in the shape of this species and in the development of the carinae. Turner (1938:93) noted the variation from faint to strong angulation found individually and stratigraphically on *Ficus remondii*, as well as on *Ficus remondii crescentensis*. Vokes (1939:152) made similar observations about *F. remondii crescentensis*, which is herein considered, along with *Ficopsis angulata* Weaver, 1905, to be morphologically indistinguishable from *F. remondii*. Weaver's holotype of *F. angulata* is a peel from an external mold of a partial specimen, and the first photograph of this peel is shown in Figure 31. The geographic and stratigraphic positions of type locality of *F. angulatus* are very poorly known.

The present writer found considerable variation in 15 specimens of *F. remondii* at LACMIP locality 22313 [= LACMIP loc. 40374] in the "Domengine Stage" part of the Llajas Formation. Regardless of size, most are tricarinate or weakly tricarinate (Fig. 34) and resemble *Priscoficus* but are missing the nodes on the carinae and also missing axial ribs. A few are bicarinate, but the bicarination can be weakly developed on one side of a specimen and somewhat stronger on its other side. Some specimens show no carinae (Fig. 36). Another specimen from the Llajas Formation is reminiscent of *Priscoficus* in that it shows wavy carinae with some widely spaced growth lines more prominent than the others (Fig. 37).

In the variable development of carinae, *F. remondii* is like two other species of *Ficus*: 1) the so-called *Ficopsis penita* (Conrad, 1833:32; Palmer, 1937:255–257, pl. 33, figs. 5–15) from middle to upper Eocene strata in Alabama and Mississippi, and 2) the so-called *Fusoficula juvenis* [not Whitfield, 1865] of Maury (1912:78, pl. 11, figs. 2, 3) from questionably lower Eocene strata in Trinidad, South America. Large collections of *Ficus penita* made by Palmer (1937) revealed that same-sized individuals (i.e., growth stage is not a factor) from the same locality can have no carinae or up to four carinae. The two specimens of "*F. juvenis*" illustrated by Maury (1912) show that there can be none or up to three carinae.

Squires (1989) and Lindberg and Squires (1990) reported that the geologic range of *F. remondii* (as *F. remondii crescentensis*) does not extend younger than the "Transition Stage." This statement is in error because *F. remondii* occurs in "Tejon Stage" strata, along with *Priscoficus hornii* in the Tejon Formation (undifferentiated) at the Edmonston Pumping Plant. These two species also occur together in "Transition Stage" or "Tejon Stage" strata in the Tejon Formation, Liveoak Shale Member (Addicott in Nilsen, 1987).

Ficus mamillata Gabb, 1864

Figures 39–41

Ficus mamillatus Gabb, 1864:211, pl. 32, fig. 276; Arnold, 1907:441, pl. 50, figs. 5a, b; English, 1914:245; Dickerson, 1915:88, pl. 6, fig. 12; Anderson and Hanna, 1925:111; Stewart, 1927:371–372, pl. 29, fig. 12; Kleinpell and Weaver, 1963:191, pl. 26, fig. 3.

Ficus mamillata Gabb. Schenck and Keen, 1940, pl. 26, fig. 4 [reproduction from Dickerson, 1915:pl. 6, fig. 12]; Givens, 1974:80–81, pl. 9, fig. 2.

EMENDED DESCRIPTION. Shell size up to height 34.5 mm and diameter 28.7 mm (same nearly complete specimen). Shell pyriform, last whorl rapidly expanding and inflated. Protoconch low conical, paucispiral (approximately two whorls), smooth. Teleoconch of 3.5 whorls. Suture slightly impressed. Spire low (approximately 18 percent of shell height). Spire angle approximately 119°. Ramp flattish. Shoulder rounded. Ornament reticulate, consisting of numerous spiral ribs and riblets intersected by weaker axial ribs. Spiral ribs fine, sharp, moderately widely spaced, with prominent rib alternating with single, much weaker spiral riblet. Axial ribs very fine, narrowly thin to squarish, and moderately widely spaced. Aperture moderately wide. Outer lip thin. Columella smooth. Siphonal canal missing. Growth line slightly opisthocline, with parasigmoidal flexure present near suture.

HOLOTYPE. ANSP 4230, type locality location not exactly known, Tejon Formation, near Fort Tejon, Kern County, California.

GEOLOGIC RANGE. Middle Eocene (middle Lutetian Stage) to lower upper Eocene (middle Priabonian Stage); equivalent to provincial "Tejon Stage" to Galvinian Stage.

GEOGRAPHIC RANGE. Southern California.

STRATIGRAPHIC DISTRIBUTION. MIDDLE EOCENE TO LOWER UPPER EOCENE ("TEJON STAGE"): Tejon Formation, Metralla Sandstone Member, Liveoak Canyon, Kern County, California (Gabb, 1864; Dickerson, 1915; Anderson and Hanna, 1925; Stewart, 1927; Addicott in Nilsen, 1987); Matilija Formation, Pine Mountain area, Ventura County, California (Givens, 1974); Matilija Formation, Nojoqui Creek area, Santa Barbara County, California (Arnold, 1907; Kleinpell and Weaver, 1963). LOWER UPPER EOCENE (GALVINIAN STAGE): Undifferentiated Sacate-Gaviota formations, Santa Barbara County, California (Weaver and Kleinpell, 1963).

REMARKS. The species is rare. Only one specimen was examined. Interribs are minor, not present on every illustrated specimen in the literature, and, if present, commonly there is only one between the principal spiral ribs.

Givens (1974) questionably reported this species from the "Transition Stage," but this assertion could not be verified. *Ficus mamillata* occurs with *Ficus remondii* in the "Tejon Stage" Tejon Formation, Metralla Sandstone Member in Liveoak Canyon, Tehachapi Mountains, Kern County, California (Addicott in Nilsen, 1987), and in the "Tejon Stage" Matilija Sandstone in the Nojoqui Creek area, Santa Ynez Mountains, Santa Barbara County, California (Weaver and Kleinpell, 1963).

Ficus gesteri Wagner and Schilling, 1923

Figures 42–45

Ficus gesteri Wagner and Schilling, 1923:258, pl. 49, figs. 1–3; Weaver and Kleinpell, 1963:191, pl. 26, fig. 3.

?*Ficus* n. sp.? Hickman, 1980:49–50, pl. 4, figs. 14–16.

EMENDED DESCRIPTION. Shell size up to height 61.5 mm and diameter 50.1 mm (on a nearly complete specimen). Inflated fusiform or pyriform, last whorl rapidly expanding and inflated. Spire angle approximately 115°. Protoconch very low, paucispiral (1.5 whorls), smooth; transition to teleoconch information wanting. Teleoconch of 3–3.5 whorls. Suture flush? Spire low.

Ramp difficult to distinguish from rounded, sloping shoulder. Ornament reticulate, consisting of numerous spiral ribs/riblets intersected by weaker axial ribs. Spiral ribs fine to medium strength, moderately widely spaced, with three much weaker spiral riblets on interspaces; spiral ribs minutely nodose at intersections with axial riblets; spiral riblets very minutely nodose at intersections with axial riblets. Spiral ribs on neck alternate with single spiral riblet on interspaces, reticulation becoming obsolete. Axial ribs very fine, closely spaced. Irregular axial swellings and some ridges on last whorl. Aperture wide. Columella smooth. Siphonal canal long, very slightly flexed, and apparently twisted anteriorly. Growth line slightly opisthocline, with parasigmoidal flexure present near suture.

TYPES. Holotype UCMP 11425, UCMP loc. 3182 and paratype UCMP 11426, UCMP loc. 3182 (both from San Emigdio Formation, San Emigdio Mountains, Kern County, California).

GEOLOGIC RANGE. Upper Eocene (Priabonian Stage) to lower Oligocene (Rupelian Stage); equivalent to Galvinian Stage.

GEOGRAPHIC RANGE. Southern California; questionably northwestern Oregon.

STRATIGRAPHIC DISTRIBUTION. UPPER EOCENE TO LOWER OLIGOCENE (GALVINIAN STAGE): Questionably Keasey Formation, Vernonia area, northwestern Oregon (Hickman, 1980); lower Gaviota Formation (LACMIP loc. 7266), Gaviota Canyon, Santa Ynez Mountains, Santa Barbara County, California (new information); upper Gaviota Formation and Sacate-Gaviota undifferentiated formations, west of Gaviota Canyon, western Santa Ynez Mountains, Santa Barbara County, California (Weaver and Kleinpell, 1963); San Emigdio Formation, San Emigdio Canyon, Kern County, California (Wagner and Schilling, 1923; Addicott in Nilsen, 1987).

REMARKS. The examined material consisted of 52 specimens. Nearly all are internal molds (steinkerns), and many are slightly crushed. The majority of the specimens are from the lower Gaviota Formation. In spite of the poor preservation, the steinkerns show details of the interrib ornamentation. At several localities in this formation, there are growth series of this species. The "nodes" reported by Hickman (1980) as being present on this species are actually elongate, irregular axial swellings that can extend across the last whorl.

Ficus n. sp.? Hickman (1980:40–50, pl. 4, figs. 14–16) known from a single specimen collected from the upper Eocene to lower Oligocene Keasey Formation in Oregon, might questionably be *Ficus gesteri*, but more specimens of the Keasey Formation ficid are needed to confirm this assertion. *Ficus* n. sp.? Hickman has relatively wide interspaces with a single interspace spiral. *Ficus gesteri* commonly has wide to very wide interspaces and commonly there are three weaker interspace spirals between two prominent spirals, but on the same specimen this pattern of ornamentation can change laterally into the same pattern seen on *Ficus* n. sp.?. It is just a matter of the middle interspace spiral becoming slightly more prominent.

Wagner and Schilling (1923) reported *F. gesteri* as occurring only in the San Emigdio Formation. They made this assertion three times in their paper: 1) in their comments about the stratigraphic occurrence of *F. gesteri*, 2) in their checklist of mollusks found in the San Emigdio Formation, and 3) on their geologic map that has the type locality (UCMP loc. 3182) plotted. In their locality description at the end of their paper, however, they mistakenly listed the type locality as being the overlying and slightly younger Pleito Formation. In their checklist of mollusks from this particular formation, there is no listing of *F. gesteri*. Their erroneous Pleito Formation occurrence also shows up on the UCMP labels in the specimen boxes containing the holotype and paratype of *F. gesteri*.

Ficus modesta (Conrad, 1848)

Figures 46–47

Pyrula modesta Conrad, 1848:433, fig. 12 [figure reprinted in Dall, 1909:151, fig. 12].

Ficus modesta (Conrad). Meek, 1864:183; Moore, 1963:32–33, pl. 3, figs. 9, 10; pl. 4, fig. 3; Hickman, 1969:88–89, pl. 12, figs. 5–8; Moore, 1971:28, pl, 9, figs. 1, 2 [reproductions from Moore, 1963:pl. 3, figs. 9, 10]; Moore and Addicott, 1987:table 1, pl. 4, fig. 2; Moore, 1994:35, pl. 3, figs. 1, 2 [reproductions from Moore, 1963:pl. 3, figs. 9, 10]; Moore, 2000:76, two unnumbered figures [reproductions from Moore, 1963:pl. 3, figs. 9, 10].

Sycotyphus modestus (Conrad). Conrad, 1865a:151.

Ficus pyriformis Gabb, 1869:48, pl. 14, fig. 4; English, 1914: 246, pl. 25, fig. 1.

Ficopsis modesta (Conrad). Gabb, 1869:113.

Ficus modestus (Conrad). Dall, 1909:74; English, 1914:246; Stewart, 1927:372–373, pl. 31, fig. 2; Etherington, 1931:96, pl. 11, fig. 6; Weaver, 1942:395–396, pl. 77, fig. 1; pl. 103, fig. 1; Hall, 1958:56, pl. 11, fig. 3; Addicott, 1976:22, pl. 1, figs. 29, 30.

Ficus wynoochensis Weaver, 1916:45–46, pl. 3, figs. 38, 39.

Ficus restorationensis Van Winkle, 1918:88, pl. 7, fig. 20.

Ficus (*Trophonsycon*) *restorationensis* Van Winkle. Weaver, 1942:397, pl. 77, fig. 13.

Ficus (*Trophonsycon*) *wynoochensis* Weaver. Weaver, 1942:398, pl. 77, fig. 4.

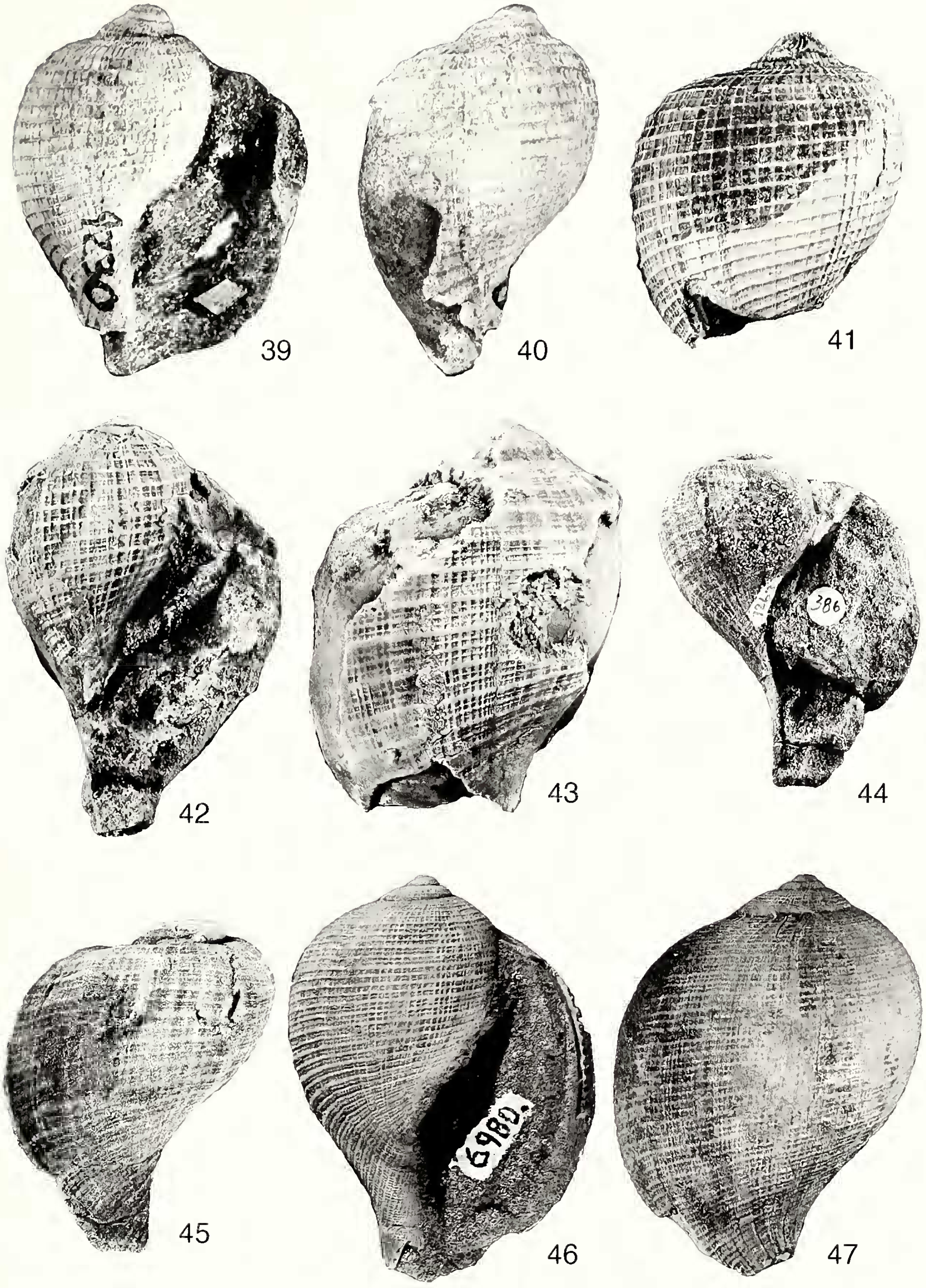
?*Ficus* cf. *F. modesta* (Conrad). Addicott, 1972:table 1, pl. 1, fig. 5; Addicott, 1973:20, pl. 9, figs. 18, 19.

EMENDED DESCRIPTION. Shell size up to height 86 mm and diameter 47 mm (on a nearly complete specimen). Shell fusiform to pyriform, last whorl rapidly expanding. Spire angle 100°–140° (commonly approximately 115°). Spire very low (nearly flat) to low (approximately 13 percent of shell height). Protoconch slightly sunken, paucispiral, approximately 1.5 whorls, smooth. Teleoconch of 2.5–3.5 whorls. Suture impressed. Ramp difficult to distinguish from rounded, sloping shoulder. Ornament reticulate, consisting of numerous spiral ribs and numerous, less prominent axial ribs. Spiral ribs very fine and very closely spaced; prominent rib alternating with single, weaker spiral riblet or riblet absent. Axial ribs very fine and closely spaced. Reticulation becoming finer on neck. Aperture wide. Columella smooth. Siphonal canal long, broadly curved, bends dorsally, narrowly notched, and twisted anteriorly. Growth line slightly opisthocline, with parasigmoidal flexure present near suture.

TYPES. Of *Pyrula modesta* Conrad, 1848, USNM 110457 (lost, according to Dall, 1909 and Moore, 1963), Astoria Formation, Astoria, Clatsop County, Oregon. Of *Ficus pyriformis* Gabb, 1869, ANSP 4325, Martinez area, Contra Costa County, California. Of *Ficus wynoochensis* Weaver, 1916, CAS 556, Astoria Formation, cuts along highway and in bank of Wynoochee River, 1.6 km south of junction with Bitter Creek, Grays Harbor County, Washington. Of *Ficus restorationensis* Van Winkle, 1918, CAS 7526, Blakeley Formation, Restoration Point, opposite Seattle, Kitsap County, Washington.

GEOLOGIC RANGE. Lowermost Oligocene (lower Rupelian) to lower Miocene (Burdigalian); equivalent to provincial Galvinian Stage to Newportian Stage.

GEOGRAPHIC RANGE. Washington to southern-central California.



Figures 39–47 Eocene, Oligocene, and Miocene *Ficus* species from coastal-western North America. 39–41. *Ficus mamillata* Gabb, 1864. 39–40. Holotype ANSP 4230, near Fort Tejon, Kern Co., California, (Tejon Formation), height 18.8 mm, ×2.9: 39. apertural view; 40. abapertural view. 41. Hypotype LACMIP 14489, LACMIP loc. 41206 (Tejon Formation, Metralla Sandstone Member), abapertural view, height 35 mm, ×1.3. 42–45. *Ficus gesteri* Wagner and Schilling, 1923. 42. Holotype UCMP 11425, UCMP loc. 3182 (San Emigdio Formation), apertural view, height 34.7 mm, ×1.8; 43. Paratype UCMP 11426, UCMP loc. 3182 (San Emigdio Formation), abapertural view, height 35.1 mm, ×1.7; 44–45. Hypotype LACMIP 14490, LACMIP loc. 7263 (Gaviota Formation, lower part), height 52 mm, ×1: 44. apertural view; 45. abapertural view. 46–47. *Ficus modesta* (Conrad, 1848), hypotype LACMIP 14491, LACMIP loc. 6980 (Astoria Formation), height 33.4 mm, ×1.8: 46. apertural view; 47. abapertural view.

STRATIGRAPHIC DISTRIBUTION. LOWER OLIGOCENE (GALVINIAN STAGE): Upper Pleito Formation, San Emigdio Canyon, Kern County, California (Wagner and Schilling, 1923). UPPER LOWER OLIGOCENE (MATLOCKIAN STAGE): Blakeley Formation, Kitsap County, Washington (Weaver, 1942); Eugene Formation, Salem, Polk County, Oregon (Hickman, 1969); lower sandstone member, Vaqueros? Formation, at The Indians (Indians Ranch), Santa Lucia Range, Monterey County, California (Addicott, 1979); Temblor Formation, Wygal Sandstone Member [= *Phacoides* Sand Member], Temblor Range, San Luis Obispo County, California (Addicott, 1972, 1973). UPPER OLIGOCENE (JUANIAN STAGE) TO LOWER MIOCENE (NEWPORTIAN STAGE): Nye Mudstone, Newport, Lincoln County, Oregon (Moore, 1963). UPPERMOST OLIGOCENE TO LOWERMOST MIOCENE (PILLARIAN STAGE): Clallam Formation, Slip Point, Olympic Peninsula, Clallam County, Washington (Addicott, 1976). LOWER MIOCENE (NEWPORTIAN STAGE): Astoria Formation, Grays Harbor County, Washington (Weaver, 1942); Astoria Formation, Astoria townsite, Clatsop County, Oregon; Tillamook Bay, Tillamook County, Oregon; Newport, Lincoln County, Oregon; and Coos Bay, Coos County, Oregon (Moore, 1963).

REMARKS. The examined material consisted of 10 specimens. *Ficus modesta* is an uncommon species. Oligocene strata yield few specimens, whereas specimens are more plentiful in the Miocene Astoria Formation. Preservation in the Astoria Formation is generally good to excellent, and the specimens have their shells intact. Insightful comments regarding the morphology of the synonyms of this species have been reported by Moore (1963) and by Hickman (1969). *Ficus modesta* shows considerable morphologic variation in its shape and spire height. For the most striking differences, see Moore (1963:pl. 3, figs. 9, 10), for illustrations of two specimens from the Astoria Formation in Oregon.

Loel and Corey (1932:pl. 48, fig. 14) reported *Ficus* cf. *modestus* from the lower Miocene Vaqueros in the Santa Clara River Valley, Ventura County, California, but the specimen is a steinkern, and specific identification cannot be made.

A ficid from the lower Miocene Clallum Formation along the north shore of the Olympic Peninsula, Washington, was originally referred to as *Ficus clallamensis* Weaver (1912:74, pl. 9, fig. 3) and characterized by a row of distinct, large, and vertically elongate nodes on the shoulder of the last whorl and another row near where the last whorl begins to become constricted. Addicott (1976:23, pl. 1, fig. 31; pl. 2, fig. 34) identified Weaver's species as *Trophosycon clallamensis* and reported that the two rows of nodes distinguish *T. clallamensis* from *F. modesta*.

A ficid from the Miocene *Scutella breweriana* zone at the top of the Monterey Group on San Pablo Bay, east of San Francisco, California was originally referred to as *Ficus rodeoensis* English (1914:246–247:pl. 24, fig. 1). It is known only from a poorly preserved steinkern. Grant and Gale (1931:751) reported that this specimen is probably a *Trophosycon* and might be a variety of *T. clallamensis*.

PHYLOGENETIC IMPLICATIONS

It is conceivable that the mid-Maastrichtian *Bulbificopsis*, a strongly carinate and strongly noded genus, was the predecessor of the Paleocene *Urosyca*, but a more complete fossil record of upper Maastrichtian to Danian ficids is necessary to confirm this assertion. *Priscoficus cooperiana* might have evolved from *U. caudata*, with the result that the spire angle decreased and spire height increased. *Priscoficus cooperiana* could have evolved, however, from a high-spire lineage of *Priscoficus* that originated elsewhere. *Priscoficus cooperiana* evolved into *P. hornii*, which in turn, evolved into *P. cowlitzensis*. The following three early Eocene species of *Priscoficus* apparently comprise another lineage: *Priscoficus tricostata* Deshayes, 1835, from France; *Priscoficus tritiara* Gardner, 1939 [possibly conspecific with *P. juvenis*], from northern Mexico; and *Priscoficus juvenis* Whitfield, 1865, from Alabama. They are unusual *Priscoficus* in that they all have a prominently angulate and strongly noded penultimate whorl.

Ficus shows a gradational change in shape through time. The early Eocene forms seem to be intermediate in morphology with *Priscoficus*. The earliest gastropod to show this intermediate morphology is *Ficus multiformis* Wrigley, 1929, which King (1981:38, fig. 52) reported as being from the early Eocene (early middle Ypresian Stage), lower NP12 calcareous nannofossil Zone, Division C of the London Clay, England. This species has a very wide range of morphology that includes shells with *Priscoficus*-like features (moderately high spire, prominent axial ribs crossed by many carinae with minutely noded intersections) and shells with more traditionally known *Ficus*-like features (moderately low spire, ornament only reticulated and without axial ribs and nodes, absence of carinae). Wrigley (1929:243) stated that the variants of *F. multiformis* are connected by a "bewildering series of intermediate forms," with many of the forms in association with each other. Some variants (see Wrigley, 1929:pl. 16, figs. 17, 20) are similar to *Priscoficus*, whereas other variants of *F. multiformis* (see Wrigley, 1929:pl. 16, figs. 15, 16a = his "typical" forms) are similar to *Ficus*.

Four other Eocene species of *Ficus* also have a considerable range of morphology that includes shells with *Priscoficus*-like features and shells with *Ficus*-like features. These species, listed in chronological order, are: *Ficus remondii* (Gabb) from middle Ypresian Stage to middle Lutetian Stage strata (equivalent to mid to upper NP12 to NP15 calcareous nannofossil zones; see Fig. 2 for ages of these zones) from coastal-western North America; *Ficus nucleoides* Garvie, 1996, from the middle Ypresian Stage Reklaw Formation (equivalent to upper NP12 to NP13), east and central Texas (Garvie, 1996); *Ficus penita* Conrad, 1833, from the upper Bartonian Stage Gosport Sand (equivalent to lower NP17) of Alabama (Palmer and Brann, 1966:678–679; Dockery, 1986:fig. 1); and *Ficus* "*juvenis*" [not Whitfield] of Maury, 1912, from presumably Eocene strata in Trinidad (Maury, 1912:30, as *Fusoficula juvenis*). *Ficus penita* represents the last vestiges of this group of gastropods with both *Priscoficus*- and *Ficus*-like features, and the last species to have any possible remnants of a carina or carinae on the last whorl.

Stemming from the early Eocene, *Ficus* shells generally evolved from having a lowly inflated last whorl with a somewhat low to moderately low spire and uniform-reticulate ornament into a pyriform shape with a low spire and variable-strength reticulate ornament. This evolution was slow, conservative, and subtle. Middle to late Eocene species generally have a cylindrical shape, somewhat low to moderately low spire, and uniform-strength reticulate ornament. Oligocene species are more inflated with a low spire and some differentiation of the strength of the spiral ribs, but some are like the Eocene forms. Miocene, Pliocene, and Holocene species are mostly pyriform with a very low to low spire, but a few species have a slightly higher spire. Difficulty in trying to evaluate the evolutionary patterns is compounded by the fact that in some species, there are a few individuals, which, other than being larger, are very similar to geologically earlier species. A good example is the Miocene *F. modesta*. Most individuals of this species have an inflated shape with a low spire, but a few individuals look very

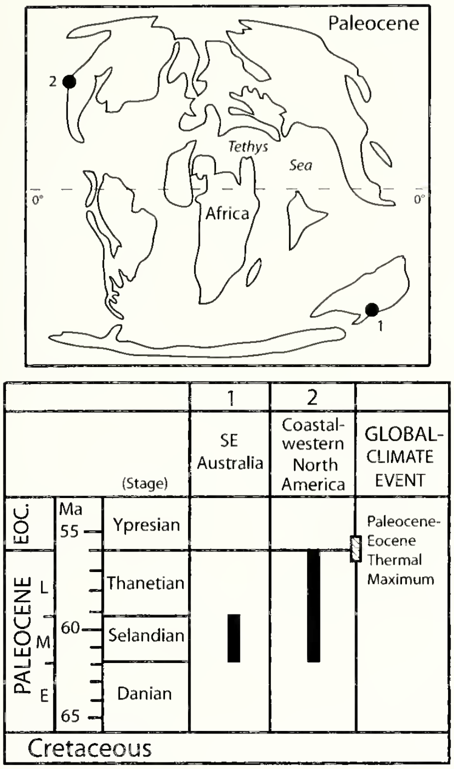


Figure 48 Global paleogeographic distribution and associated temporal ranges of *Urosyca*; data derived from Table 1. Geologic time scale, stage ages, and timing of global climate events from Gradstein et al. (2012:fig. 28.11). Maps modified from Smith et al. (1994) show land masses. Solid circles = *Urosyca* occurrences; thick vertical lines indicate *Urosyca* temporal ranges. Numbers at top of columns refer to geographic regions and primary sources of data: 1) Darragh (1997). 2) present study.

similar to Eocene forms. The occurrence of previous shapes seems to suggest that local paleoenvironmental factors had a role in determining shell shape. Attempts herein to recognize distinct lineages of *Ficus* were unsuccessful because of the subtlety of the morphologic gradations and the occurrence of previous shell shapes.

The complexity of the evolution of *Ficus* has also been noted by other workers. Woodring (1959:210–211) discussed that it has long been recognized that late Cenozoic to Holocene *Ficus* in the Caribbean Sea region can be classified into two groups: the *Ficus papyratia* (Say, 1822) group [referred to as *F. communis* group by Woodring] and the *Ficus ventricosa* (Sowerby, 1825b) group. Both groups reportedly comprise a so-called "complex of species (± subspecies)." Verhaeghe and Poppe (2000:17–18) discussed the *F. papyratia* group and its various subspecies. Woodring (1959:212), Jung (1965:517), and DeVries (1997:14) discussed the *Ficus ventricosa* group, which has the principally Miocene *Ficus carbasea* (Guppy, 1866) as one end member of the complex and the Pliocene to Holocene *F. ventricosa* as the other end member. Genetic studies are needed to determine how many of the dozen or so living species of *Ficus* are biologic species and how many are ecologically influenced variants.

Another evolutionary trend in *Ficus* is its gradual increase in shell size. The genus attained its greatest size during the Holocene, with shells up to 160 mm high (Verhaeghe and Poppe, 2000) and having a low spire. It is possible that the shortening of the spire and increase in shell size afforded *Ficus* more ability to resist predation.

GLOBAL PALEOBIOGEOGRAPHY AND PALEOCLIMATIC IMPLICATIONS

The global distribution of *Urosyca*, *Priscoficus*, and *Ficus* is shown in Figures 48–50, respectively, and these charts are based on data compiled in Tables 1–3, respectively. *Urosyca* is restricted to the Paleocene, and only three species are known. The genus appeared simultaneously during the middle Paleocene in southeastern Australia and California, resulting in an amphitropic distribution (Fig. 48). Although it disappeared from Australia before the late Paleocene, it remained in California during the late Paleocene, until it went extinct toward the end of that epoch.

Priscoficus ranges from the late early Paleocene to early Miocene, and 22 species are known (Table 2). Its earliest known occurrence is an unnamed species from the Agatdal Formation, West Greenland. Schnetler and Petit (2010:4) reported this formation to be of late early to questionably early middle Paleocene age. During the late Paleocene, *Priscoficus* spread southward in the northern Atlantic region and occurred in Europe, Maryland, Virginia, Alabama, and northern Mexico. The early Eocene lineage of *Priscoficus tricostata* Deshayes, 1835, from France; *Priscoficus juvenis* Whitfield, 1865, from Alabama; and *Priscoficus tritiara* Gardner, 1939, from northern Mexico is evidence of early Eocene dispersal of this genus via currents flowing westward from the Tethys Sea region toward the eastern coast of the United States.

Priscoficus was most widespread two times: during the late Paleocene to early Eocene Thermal Event (PETM) and during the late middle Eocene (Fig. 2). The genus occurred only in the Northern Hemisphere during the Paleocene, but during the Eocene the genus had an amphitropical distribution, with occurrences in somewhat constrained northern and southern latitudinal components separated by a distinct and broad equatorial gap (Fig. 49). During the late middle Eocene, the genus also reached both Kamchatka and New Zealand for the first time.

During the Paleocene through middle Eocene, nearly all the shallow marine gastropods of coastal-western North America were thermophilic taxa (Squires, 2003:29). *Priscoficus cowlitzensis*, the last *Priscoficus* on coastal-western North America,

Table 1 Species assigned herein to *Urosyca*, with age and geographic distribution.

Urosyca species	Age	Location
caudata Gabb, 1869	Middle to late Paleocene	California and N Baja
quadrifunifer Darragh, 1997	Paleocene (undifferentiated)	SE Australia
robusta Weaver, 1905	Middle Paleocene	California

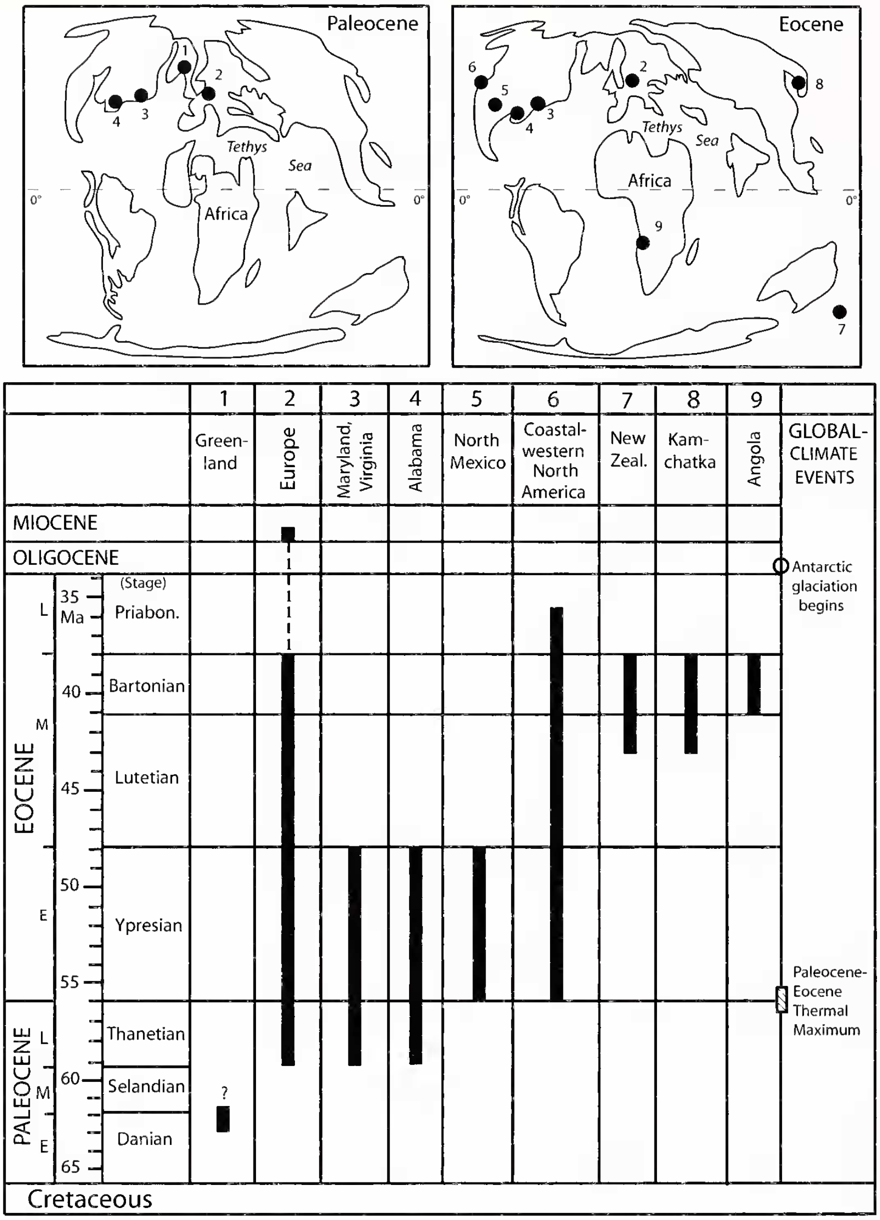


Figure 49 Global paleogeographic distribution and associated temporal ranges of *Priscoficus* (plotted in order of first-appearance datum); data derived from Table 2. Geologic time scale, stage ages, and timing of global climate events from Gradstein et al. (2012:fig. 28.11). Maps modified from Smith et al. (1994) show land masses. Solid circles = *Priscoficus* occurrences; thick vertical lines indicate *Priscoficus* temporal ranges. Numbers at top of columns refer to geographic regions and primary sources of data: 1, Kollmann and Peel (1983); 2, Wrigley (1929), King (1981), Karagiuleva (1964), Pfister and Wegmüller (2007), Quaggiotto and Mellini (2008), Zunino and Pavia (2009); 3 and 4, Palmer and Brann (1966); 5, Gardner (1939); 6, present study; 7, Marwick (1942, 1960), Beu and Maxwell (1990); 8, Sinelnikova et al. (1991); 9, Caster (1938).

is a very abundant faunal element in the upper middle Eocene Cowlitz Formation of Washington. Nearly all the gastropod genera in this formation have been found elsewhere in coastal-western North America in older warm-water deposits (Squires, 2003:27). According to Nesbitt (1995:1060, 1063), the Cowlitz Formation macrofauna and microfauna both represent subtropical conditions. At about 37 Ma, near the boundary of the "Tejon Stage" and the Galvinian Stage, a faunal change occurred. This change, referred to as a "turnover" event by Squires (2003), was near the time of the beginning of glaciation in Antarctica. The reported tentative occurrence of *P. cowlitzensis* reported from the uppermost Eocene Gaviota Formation of Southern California (Weaver and Kleinpell, 1963) suggests that this species, in response to cooling waters to the north, retreated southward from Washington during the latest Eocene. *Priscoficus* greatly declined worldwide after the late Eocene with the start of the Antarctic glaciation and associated ocean cooling. No Oligocene record of this genus was detected in the literature. Only a single

Table 2 Species assigned herein to *Priscoficus*, with age and geographic distribution.

Priscoficus species	Age	Location
alectodens Marwick, 1942	Late middle Eocene	New Zealand
allani Marwick, 1960	Middle Eocene	New Zealand
arguta Clark, 1896	Late Paleocene to early Eocene	Maryland, Virginia
bicarinata Briart and Cornet, 1871	Early Eocene	France
burdigalensis G.B. Sowerby I, 1825a	Early Miocene	France, Italy, Austria
cooperiana Stewart, 1927	Early to middle Eocene	California
cowlitzensis Weaver, 1912	Late middle Eocene	Washington, Oregon, ?Alaska
eocenica Wrigley, 1929	Middle Eocene	England
gradata Vinassa de Regny, 1896	Eocene (undifferentiated)	Northern Italy
harrisi Caster, 1938	Late middle Eocene	Angola
hornii Gabb, 1864	Mid to late Eocene	Washington, Oregon, California, ?Alaska
intermedia Melleville, 1843	Late Paleocene	France, Bulgaria
juvenis Whitfield, 1865	Early Eocene	Alabama
londini Wrigley, 1929	Middle? Eocene	England
nodulifera G.B. Sowerby II, 1859	Eocene (undifferentiated)	England
smithi J.D.C. Sowerby, 1827	Early Eocene	England
tricostata Deshayes, 1835	Early Eocene	France
tritiara Gardner, 1939	Early Eocene	Northern Mexico
tuberculata Oleinik in Sinelnikova et al., 1991	Middle to late middle Eocene	Western Kamchatka
triserialis Whitfield, 1865	Early Eocene	Alabama
vincenti Wrigley, 1929	Middle? Eocene	England
Fulguroficus sp. of Kollmann and Peel, 1983	Late early to ?middle Paleocene	West Greenland

relictual species is known from lower Miocene strata in Europe (Harzhauser, 2002).

Ficus ranges from the early Eocene to Holocene, and there are at least 70 species with a fossil record (Table 3). As mentioned above, its earliest known occurrences that can be confirmed are of early Eocene age in England, California, and Texas. Based on locality and geologic details given by Wrigley (1929) and King (1981), the occurrence in England is slightly older than the occurrence in California, which is slightly older than the Texas occurrence. These three occurrences were just after the PETM event. England appears to have been the point of origin of *Ficus*, with the prevalent westward-flowing equatorial current during the Eocene (see Squires, 1987) allowing *Ficus* to spread from England to North America. By the late Eocene, *Ficus* had dispersed throughout much of the world. Although it did extend into the Southern Hemisphere, the genus is found predominantly in the Northern Hemisphere (Fig. 50). Based on the information found during this present report (Table 3; Fig. 50), *Ficus* survived the cooling event associated with the beginning of the Antarctic glaciation at the beginning of the Oligocene.

Occurrences of extinct species of *Ficus* are nearly universally cited as indicative of tropical/warm-water conditions because extant species mostly live in tropical equatorial waters. Based on the information obtained during this present investigation, *Ficus* did not live in such waters during the Paleocene to late middle Eocene. During the late Eocene to early Miocene, for example, it lived in cooler waters, mainly in Oregon and Washington. The paleoclimatic implications of this genus being found in the upper Eocene middle member of the Keasey Formation in Oregon (Hickman, 1980), Oligocene Eugene Formation in Oregon (Hickman, 1969), and the lower Miocene Clallam Formation in Washington (Addicott, 1976) have been noted by these workers. Hickman (1980:50) stated that the presence of *Ficus* in the Keasey Formation "suggests broader Paleogene bathymetric and temperature ranges" relative to the "tropical, warm-adapted forms" of this genus. Hickman (1969:89) stated that the occurrence of *Ficus* "with more typically temperate forms in the Oligocene and Miocene suggests either that it was a relictual faunal element or that the genus as a whole had a wider range of tolerance during that time."

Ficus became better established in South America during the Oligocene and Miocene. By the end of the early Miocene, which coincided with the warmest interval of the Neogene (Fig. 50) (i.e., the Mid-Miocene Climatic Optimum), *Ficus* attained its most widespread geographic distribution. Starting in the late Miocene and extending through the Pliocene, the ficid *Trophosycon* replaced *Ficus* on coastal-western North America. During the late Miocene and early Pliocene, *Ficus* preferred the Caribbean Sea region (Beu, 2010; Landau and Silva, 2010), and western South America (Anderson, 1929; Olsson, 1964; Covacevich and Frassinetti, 1983). During the Pliocene and Pleistocene, *Ficus* was nearly confined to the New World, with most of its occurrences along the southeast coast of the United States, the Caribbean Sea, and northwestern South America (Fig. 50). Not surprisingly, the Pleistocene Ice Age diminished the global extent of *Ficus*.

The fossil record of most of the extant species of *Ficus* is poorly known, and the four species with a documentable pre-Holocene record are: *F. ficus* (Linnaeus, 1758); *F. papyratia* (Say, 1822) s.l.; *F. variegata* (Röding, 1798); and *F. ventricosa* (Sowerby, 1825b) (Table 3). The latter is the only extant ficid known from coastal-western North America and is found living in shallow warm waters from Magdalena Bay along the west side of Baja California Sur, Mexico, throughout the Gulf of California, and south to Peru (Keen, 1971). *Ficus ventricosa* is known from Miocene to Pliocene beds in Southern California (Hanna, 1926:449, pl. 21, fig. 6), in the northern Gulf of California (Hertlein, 1968:403), and near the southern tip of Baja California, Sur (Hertlein, 1966:269, as cf. *F. ventricosa*). It is also known, as the synonym *Ficus decussata* (Wood, 1828), from Pleistocene beds at Magdalena Bay (Jordan, 1924:149; Grant and Gale, 1931:743). Woodring (1959:210) recognized that *F. ventricosa* represents an end member of "Group *Ficus ventricosa*" that encompasses the Miocene Caribbean *F. carbasea* (Guppy, 1866) s.l. The fossil record of this "Group" and of *F. ventricosa* are not well established. An indeterminate *Ficus* is also

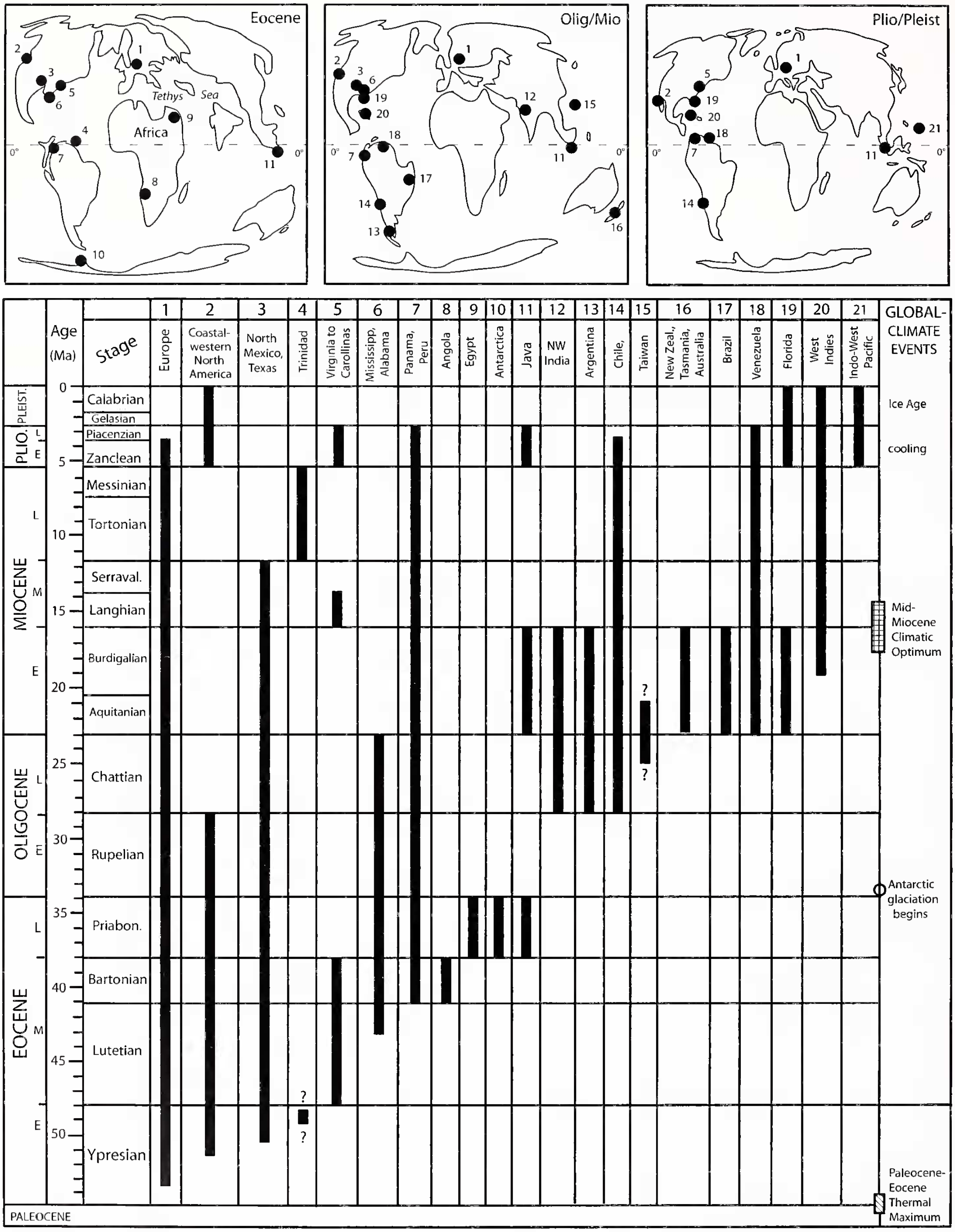


Figure 50 Global paleogeographic distribution and associated temporal ranges of *Ficus* (plotted in order of first-appearance datum); data derived from Table 1. Geologic time scale, stage ages, and timing of global climate events from Gradstein et al. (2012:fig. 28.11). Maps modified from Smith et al. (1994) show land masses. Solid circles = *Ficus* occurrences; thick vertical lines indicate *Ficus* temporal ranges. Numbers at top of columns refer to geographic regions and primary sources of data: 1, Cossmann and Pissarro (1911), Wrigley (1929), Baldi (1973), Karagiuleva (1964), Solsona (1999), Pfister and Wegmüller (2007), Harzhauser et al. (2009), Zunino and Parva (2009); 2, present study; 3, Maury (1912); 4, Harris (1919), Gardner (1939), Garvie (1996); 5, Martin (1904), Van Winkle (1919); 6, Meyer (1885), Palmer (1937, 1947); 7, Spieker (1922), Olsson (1928, 1931, 1964), Clark and Durham (1946), Woodring (1959), DeVries (1997); 8, Caster, 1938; 9, Blanckenhorn (1900), Abbass (1967); 10, Stilwell and Zinsmeister (1992); 11,

Table 3 Species assigned herein to *Ficus*, with age and geographic distribution; Holocene species without a known fossil record excluded.

Ficus species	Age	Location
affinis Van Winkle, 1919	Middle to late Eocene	Virginia, S Carolina, Maryland
allenmanae DeVries, 1997	Middle Miocene to early Pliocene	Peru, Chile
altispira Pritchard, 1896	Early Miocene	Tasmania, Australia
amichel Gardner, 1939	Late Eocene	NE Mexico
angelinensis Harris, 1919	Middle Eocene	Texas
apenninica Sacco, 1890	Eocene to early Oligocene	Italy
australis Stilwell and Zinsmeister, 1992	Late Eocene	Antarctica
austrina Stilwell and Zinsmeister, 1992	Late Eocene	Antarctica
bernardi Beu, 2010	Late early Miocene to early Pliocene	West Indies (Dominican Republic)
carbasea Guppy, 1866 *sensu lato*	Early Miocene to early Pliocene	Panama to Peru and Venezuela, Trinidad
carolina d'Orbigny, 1847	Late Oligocene to early Miocene	Chile, Argentina
carriacouensis Trechmann, 1935	Late early to early middle Miocene	West Indies
concinna Beyrich, 1854	Early to late Oligocene	Germany, Hungary
condita Brongniart, 1823	Late Oligocene	Europe, NW India
chinguensis Clark in Clark and Durham, 1946	Late Eocene	Colombia
chiraensis Olsson, 1931	Late Eocene	Peru
distans G.B. Sowerby, I, 1846	Early to early middle Miocene	Chile, Peru
elegans Lamarck, 1803	Middle to late Eocene	France
elongata Vinassa de Regny, 1896	Eocene (undifferentiated)	Italy
eopapyracea Gardner, 1947	Early Miocene	Florida
epomis Woodring, 1959	Late Oligocene	Panama
exporrecta Martin, 1931	Late Eocene	Java
ficus Linnaeus, 1758	Early Pliocene to Holocene	Indo-West Pacific
filia Meyer, 1885	Late middle Eocene	Mississippi
floridaensis Olsson and Harbison, 1953	Pliocene	Florida
fragilis Deshayes, 1864	Middle Eocene	France
gayana Covacevich and Frassinetti, 1983	Oligocene/Miocene	Chile
geometra Borson, 1825	Early Miocene to early Pliocene	Europe
gesteri Wagner and Schilling, 1923	Late Eocene	California
gibsonsmithi Beu, 2010	Late Miocene to early Pliocene	West Indies (Dominican Republic)
greenwoodi J.D.C. Sowerby, 1825	Late middle Eocene	England
harrisi Martin, 1904	Early middle Miocene	Maryland
helvetica Mayer-Eymar, 1887	Late Eocene	Bulgaria
imperfecta Marshall and Murdoch, 1919	Late early Miocene	New Zealand
jacksonensis Olsson and Harbison, 1953	Pliocene	Florida
"*juvenis*" of Maury (1912)	Early Eocene?	Trinidad
kachhensis Vredenburg, 1925	Early Miocene	NW India
lanzi Olsson, 1964	Late Pliocene	Ecuador
lisselonga Beu, 2010	Late Miocene to early Pliocene	West Indies (Dominican Republic)
mamillata Gabb, 1864	Late middle Eocene	California
mayereymari Blanckenhorn, 1900	Eocene (undifferentiated)	Egypt
menengtengana Martin, 1899	Pliocene	Java
meridionalis Stilwell and Zinsmeister, 1992	Late Eocene	Antarctica
merita Palmer, 1947	Late middle Eocene	Mississippi
mississippiensis Conrad, 1848	Early to late Oligocene	SE USA, northern Mexico
modesta Conrad, 1848	Early Oligocene to middle Miocene	California, Oregon, Washington
moharrami Abbass, 1967	Late Eocene	Egypt
multiformis Wrigley, 1929	Early Eocene	England
nexilis Solander, 1766	Early to late middle Eocene	England
nucleoides Garvie, 1996	Early Eocene	Texas
otaria Olsson, 1928	Late Eocene	Peru
pamotanensis Martin, 1899	Early Miocene	Java
panna Deshayes, 1864	Late Eocene	France
paraensis White, 1887	Early Miocene	Brazil
parva Suter, 1917	Miocene	New Zealand
papyratia Say, 1822 *sensu lato*	Pliocene to Holocene	North Carolina to Gulf of Mexico

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Martin, 1899; 12, Vredenburg (1925); 13, Covacevich and Frassinetti (1980, 1983), Chiesa et al. (1995), DeVries (1997), del Río (2004), Parras et al. (2008); 14, Yokoyama (1928), Tan (1971), Kanno and Chung (1975); 15, Pritchard (1896), Suter (1917), Marshall and Murdoch (1919), Beu and Maxwell (1990); 16, White (1887); 17, Woodring (1959); 18, Gardner (1947), Olsson and Harbison (1953); 19, Smith (1907), Trechmann (1935), Jung (1971), Beu (2010); 20, MacNeil (1961), Noda (1991), Kohn and Arua (1999).

Table 3 Continued.

Ficus species	Age	Location
penita Conrad, 1833	Late middle Eocene	Alabama, Mississippi?
perplexa Olsson, 1964	Late Pliocene	Ecuador
peruviana Spieker, 1922	Early Miocene	Peru
pilsbryi Smith, 1907	Late Pliocene	West Indies (Jamaica, Dominican Republic)
posadasensis Chiesa, Parma, and Camacho, 1995	Late Oligocene to early Miocene	Argentina
remondii Gabb, 1864	Late early to middle Eocene	California
roscheni Caster, 1938	Late middle Eocene	Angola
simplex Beyrich, 1854	Miocene	Europe
sindonata Wrigley, 1929	Late middle Eocene	England
spinelli Vinassa de Regny, 1896	Eocene (undifferentiated)	Italy
taiwanica Yokoyama, 1928	Miocene (undifferentiated)	Taiwan
takahasii Tan, 1971	Oligocene (undifferentiated)	Taiwan
tricarinata Lamarck, 1803	Middle to late Eocene	France, Bulgaria
variegata Röding, 1798	Early Pleistocene to Holocene	Indo-West Pacific
ventricosa G.B. Sowerby, I, 1825b	Pliocene to Holocene	Southern California to Peru
viejoensis Clark in Clark and Durham, 1946	Late Eocene	Colombia
woodringi Olsson, 1931	Late Oligocene	Peru

present in the upper Miocene Imperial Formation in Riverside County, Southern California (Powell, 1988).

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